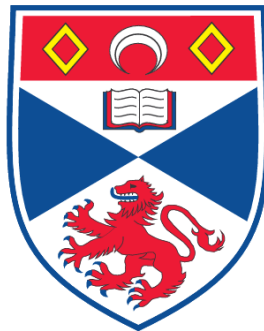


**ESTIMATING THE IMPACT OF BYCATCH AND CALCULATING
BYCATCH LIMITS TO ACHIEVE CONSERVATION OBJECTIVES
AS APPLIED TO HARBOUR PORPOISE IN THE NORTH SEA**

Arliss J. Winship

**A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews**



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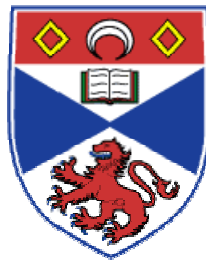
Estimating the impact of bycatch
and calculating bycatch limits
to achieve conservation objectives
as applied to harbour porpoise in the North
Sea

Arliss J. Winship


A thesis submitted for the degree of Doctor of Philosophy

School of Biology, University of St Andrews

March 2009





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Table of Contents

List of Tables	ix
List of Figures	xi
Abstract	xxiii
Acknowledgements	xxiv
Chapter 1: General Introduction	1
Bycatch, harbour porpoise and the North Sea	1
Estimating the impact of bycatch and calculating appropriate limits	4
Data	13
Thesis structure	19
Chapter 2: Standardised indices of harbour porpoise abundance in the North Sea from European Seabirds at Sea surveys.....	22
Introduction.....	22
Methods.....	24
ESAS survey methodology and database	24
Selected data	27
Statistical modelling.....	27
Variables	27
Models.....	47
Results.....	49
Best models.....	49
Year effects	62

Best models.....	62
Averaged models	65
Mixed-effects models.....	65
Discussion	69
Chapter 3: Assessment of the population dynamics and conservation status of harbour porpoise in the North Sea using an integrated model to synthesize information on life history, abundance and bycatch	
Introduction.....	75
Methods.....	77
Population model	77
Data	82
Study area.....	82
Abundance	84
Life History.....	84
Bycatch and fishing effort.....	90
Parameter estimation.....	94
Model scenarios	103
Results.....	105
Convergence	105
Density-independent model of single population	106
Scenario 1.....	106
Scenarios 2 and 3	111

Scenario 4.....	117
Scenario 5.....	117
Density-dependent model of single population	119
Scenario 6.....	119
Density-independent model of two subpopulations.....	123
Scenario 7.....	123
Scenario 8.....	127
Scenario 9.....	127
Discussion	128
Bycatch	128
Population growth rate and life history.....	133
Carrying capacity	137
Population structure	138
Future directions	140
Chapter 4: Management procedures for calculating bycatch limits for harbour porpoise in the North Sea.....	142
Introduction.....	142
Methods.....	145
Conservation objectives	145
Management procedures	147
PBR.....	148
CLA.....	149

Operating model.....	152
Tuning of the management procedures.....	164
Performance-testing simulations.....	166
Multi-subpopulation simulations	169
Implementation for harbour porpoise in the North Sea	170
Results.....	174
Tuning of the management procedures.....	174
Performance-testing simulations.....	177
First and second tunings.....	177
Third tuning	181
Historical bycatch time-series.....	181
Fishery-related performance criteria.....	184
Multi-subpopulation simulations	184
Implementation for harbour porpoise in the North Sea	184
Discussion.....	191
Which procedure?	191
Which tuning?.....	192
Further simulation testing	193
Extensions to the management procedures.....	197
Implementation	198
Chapter 5: General Discussion.....	199

Thesis summary	199
Achieving bycatch limits	202
The human side of the equation	206
Final remarks	209
Literature Cited	210

List of Tables

Table 2.1. Subsets of survey effort in the North Sea from the ESAS database analysed in this study. Latitudes and longitudes represent spatial boundaries that I applied to certain subsets. Date ranges represent the earliest and latest dates of analysed effort across all years. Numbers of ships and observers represent numbers of unique ship and observer codes. Data sources are: 1) Joint Nature Conservation Committee (UK); 2) Instituut voor Bos en Natuur (Netherlands); 3) Royal Netherlands Institute for Sea Research (NIOZ); 4) Institute of Nature Conservation (Belgium); 5) Vogelwarte Helgoland (Germany).	28
Table 2.2. Best models of number of harbour porpoise sighted per recording period selected using AIC for each data subset. All models were forced to include a year term and log(Distance) as an offset. The degrees of freedom for each term are in parentheses. NA indicates that the term was not considered for the model. Percent deviance explained was calculated as $[1-(\text{residual deviance}/\text{null deviance})]\times 100$	50
Table 3.1. Number of females by age, country, sexual maturity status, and mortality type (natural and bycatch). Data on natural mortality were not available for Denmark because probable cause of death was not established for stranded animals. Data are summarized for all years, but the model was fitted to mortality data from each year separately.	85
Table 3.2. Number of sexually mature females by pregnancy status, year, country, and health status. Animals whose probable cause of death was trauma (e.g., bycatch, bottlenose dolphin attack) were considered healthy. Years represent 1 September-31 May. Data from June-August were not considered because of the possibility that early-term foetuses were missed during examination.....	87
Table 3.3. Data on observed fishing effort and bycatch by country and fishery.	91
Table 3.4. Data on total fishing effort by country and fishery.....	92
Table 3.5. Estimated parameters of the population model. Prior probability distributions were uniform (described by a lower limit and an upper limit).	95
Table 3.6. Modelled scenarios.	104

Table 4.1. Parameters of the operating model and values used in generic performance-testing simulation trials. Baseline values are indicated by ‘*’ and ‘worst-case’ values used for the third tuning are indicated by ‘†’. Fixed parameters were held constant in all trials. In each trial the value of one bottom-level parameter was altered while keeping all others at their baseline values, and then simulations were run over all combinations of values of the top-level parameters. 154

Table 4.2. Time-series of historical bycatch input to the CLA procedure to calculate bycatch limits for harbour porpoise in the North Sea (Table 4.3). Year represents the year of life beginning in the year indicated (e.g., 1987 would represent 1 July 1987 – 30 June 1988). Bycatches for the entire North Sea are median estimates from Scenario 1 of the integrated population dynamics model presented in Chapter 3; bycatches for the northern and southern sub-areas are from Scenario 9. Note that estimates of bycatch for the northern and southern North Sea do not necessarily sum to the estimates for the entire North Sea as these sets of estimates are from different model scenarios..... 172

Table 4.3. Example bycatch limits for harbour porpoise in the North Sea using the tuned PBR and CLA management procedures. Time-series of historical bycatch input to the CLA management procedure are presented in Table 4.2..... 188

List of Figures

Figure 2.1. Distribution of survey effort among ships for data subset 2 (Table 2.1). Black bars indicate years in which individual ships were used for survey effort. Numbers within the bars indicate the percentage of total effort represented by that ship in that year.....	30
Figure 2.2. Distribution of survey effort among ships for data subset 3 (Table 2.1). Black bars indicate years in which individual ships were used for survey effort. Numbers within the bars indicate the percentage of total effort represented by that ship in that year.....	30
Figure 2.3. Distribution of survey effort among ships for data subset 5 (Table 2.1). Black bars indicate years in which individual ships were used for survey effort. Numbers within the bars indicate the percentage of total effort represented by that ship in that year.....	31
Figure 2.4. Distribution of survey effort among ships for data subset 7 (Table 2.1). Black bars indicate years in which individual ships were used for survey effort. Numbers within the bars indicate the percentage of total effort represented by that ship in that year.....	32
Figure 2.5. Distribution of survey effort among observers for data subset 1 (Table 2.1). Black bars indicate years in which individual observers had survey effort. Numbers within the bars indicate the percentage of total effort represented by that observer in that year.....	32
Figure 2.6. Distribution of survey effort among observers for data subset 2 (Table 2.1). Black bars indicate years in which individual observers had survey effort. Numbers within the bars indicate the percentage of total effort represented by that observer in that year.....	33
Figure 2.7. Distribution of survey effort among observers for data subset 3 (Table 2.1). Black bars indicate years in which individual observers had survey effort. Numbers within the bars indicate the percentage of total effort represented by that observer in that year.....	34

Figure 2.8. Distribution of survey effort among observers for data subset 4 (Table 2.1). Black bars indicate years in which individual observers had survey effort. Numbers within the bars indicate the percentage of total effort represented by that observer in that year..... 34

Figure 2.9. Distribution of survey effort among observers for data subset 5 (Table 2.1). Black bars indicate years in which individual observers had survey effort. Numbers within the bars indicate the percentage of total effort represented by that observer in that year..... 35

Figure 2.10. Distribution of survey effort among observers for data subset 6 (Table 2.1). Black bars indicate years in which individual observers had survey effort. Numbers within the bars indicate the percentage of total effort represented by that observer in that year..... 36

Figure 2.11. Distribution of survey effort among observers for data subset 7 (Table 2.1). Black bars indicate years in which individual observers had survey effort. Numbers within the bars indicate the percentage of total effort represented by that observer in that year..... 37

Figure 2.12. Geographic distribution of survey effort and harbour porpoise sightings by year for data subset 1 (Table 2.1). Coloured area indicates survey effort and red circles indicate recording periods with sightings. The size of a circle is proportional to the number of animals sighted during that recording period (scaled to the power of 0.4 for illustrative purposes). Number of recording periods with sightings (n) and the percentage of recording periods with sightings are indicated for each year..... 38

Figure 2.13. Geographic distribution of survey effort and harbour porpoise sightings by year for data subset 2 (Table 2.1). Coloured area indicates survey effort and red circles indicate recording periods with sightings. The size of a circle is proportional to the number of animals sighted during that recording period (scaled to the power of 0.4 for illustrative purposes). Number of recording periods with sightings (n) and the percentage of recording periods with sightings are indicated for each year. Survey effort colour legend is shown in Fig. 2.12. 39

Figure 2.14. Geographic distribution of survey effort and harbour porpoise sightings by year for data subset 3 (Table 2.1). Coloured area indicates survey effort and red circles indicate recording periods with sightings. The size of a circle is proportional to the number of animals sighted during that recording period (scaled to the power of 0.4 for illustrative purposes). Number of recording periods with sightings (n) and the percentage of recording periods with sightings are indicated for each year. Survey effort colour legend is shown in Fig. 2.12. 40

Figure 2.15. Geographic distribution of survey effort and harbour porpoise sightings by year for data subset 4 (Table 2.1). Coloured area indicates survey effort and red circles indicate recording periods with sightings. The size of a circle is proportional to the number of animals sighted during that recording period (scaled to the power of 0.4 for illustrative purposes). Number of recording periods with sightings (n) and the percentage of recording periods with sightings are indicated for each year. Survey effort colour legend is shown in Fig. 2.12. 41

Figure 2.16. Geographic distribution of survey effort and harbour porpoise sightings by year for data subset 5 (Table 2.1). Coloured area indicates survey effort and red circles indicate recording periods with sightings. The size of a circle is proportional to the number of animals sighted during that recording period (scaled to the power of 0.4 for illustrative purposes). Number of recording periods with sightings (n) and the percentage of recording periods with sightings are indicated for each year. Survey effort colour legend is shown in Fig. 2.12. 42

Figure 2.17. Geographic distribution of survey effort and harbour porpoise sightings by year for data subset 6 (Table 2.1). Coloured area indicates survey effort and red circles indicate recording periods with sightings. The size of a circle is proportional to the number of animals sighted during that recording period (scaled to the power of 0.4 for illustrative purposes). Number of recording periods with sightings (n) and the percentage of recording periods with sightings are indicated for each year. Survey effort colour legend is shown in Fig. 2.12. 43

Figure 2.18. Geographic distribution of survey effort and harbour porpoise sightings by year for data subset 7 (Table 2.1). Coloured area indicates survey effort and red circles indicate recording periods with sightings. The size of a circle is proportional to

the number of animals sighted during that recording period (scaled to the power of 0.4 for illustrative purposes). Number of recording periods with sightings (*n*) and the percentage of recording periods with sightings are indicated for each year. Survey effort colour legend is shown in Fig. 2.12. 44

Figure 2.19. Geographic distribution of survey effort and harbour porpoise sightings for each data subset (Table 2.1). Light grey area indicates survey effort and black points indicate recording periods with sightings. Number of recording periods with sightings (*n*) and the percentage of recording periods with sightings are indicated for each subset. 45

Figure 2.20. Effect of sea state on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Solid lines indicate the estimated mean sighting rate and dashed lines indicate the mean \pm 1 standard error (calculated on the scale of the link function and then converted to the response scale). 54

Figure 2.21. Effect of visibility on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Effects are only shown for models that had a visibility term (Table 2.2). Visibility code A represents the poorest visibility which increases to the best visibility at code D. Solid points indicate the estimated mean sighting rate and dashed lines indicate the mean \pm 1 standard error (calculated on the scale of the link function and then converted to the response scale). 55

Figure 2.22. Effect of number of observers on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Effects are only shown for models that had a number of observers term (Table 2.2). Solid points indicate the estimated mean sighting rate and dashed lines indicate the mean \pm 1 standard error (calculated on the scale of the link function and then converted to the response scale). 55

Figure 2.23. Effect of bird count type on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Effects are only shown for models that had a bird count type term (Table 2.2). Solid points indicate the estimated mean sighting rate and dashed lines indicate the mean \pm

1 standard error (calculated on the scale of the link function and then converted to the response scale).56

Figure 2.24. Effect of estimated speed on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Effects are only shown for models that had a speed term (Table 2.2). Solid lines indicate the estimated mean sighting rate and dashed lines indicate the mean \pm 1 standard error (calculated on the scale of the link function and then converted to the response scale).57

Figure 2.25. Effect of relative time of daylight on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Effects are only shown for models that had a relative time of daylight term (Table 2.2). A relative time of daylight of -1 corresponds to sunrise and 1 corresponds to sunset. Solid lines indicate the estimated mean sighting rate and dashed lines indicate the mean \pm 1 standard error (calculated on the scale of the link function and then converted to the response scale).58

Figure 2.26. Effect of day of year on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Effects are only shown for models that had a day of year term (Table 2.2). Note that the effect of day of the year varied with longitude and latitude for subset 5 (the effect shown is for the mean longitude and latitude—7.8°E, 54.2°N). Solid lines indicate the estimated mean sighting rate and dashed lines indicate the mean \pm 1 standard error (calculated on the scale of the link function and then converted to the response scale).60

Figure 2.27. Relative effect of longitude and latitude on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top left corner of each panel; Table 2.1). Note that the effects of longitude and latitude varied with day of the year for subset 5 (the effect shown is for the mean day of the year—25 June).61

Figure 2.28. Effect of year on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Black points indicate the estimated mean sighting rate and dashed lines indicate the mean \pm 1 standard error (calculated on the scale of the link function and then converted to the

response scale). Grey points indicate years with no sightings which were not modelled and in some cases were represented by few data. 63

Figure 2.29. Histogram of CVs of year effects for all best models (Table 2.2). CVs were calculated assuming that the errors in estimated effects were normally distributed on the scale of the link function (log) so that $CV = \sqrt{e^{\sigma^2} - 1}$ where σ is the standard error on the scale of the link function. 64

Figure 2.30. Model-averaged effect of year on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Solid points indicate the estimated mean sighting rate and dashed lines indicate the mean ± 1 standard error (calculated on the scale of the link function and then converted to the response scale). Note that years with no sightings are not shown. ... 66

Figure 2.31. Histogram of CVs of model-averaged year effects. CVs were calculated assuming that the model-averaged errors in estimated effects were normally distributed on the scale of the link function (log) so that $CV = \sqrt{e^{\sigma^2} - 1}$ where σ is the model-averaged standard error on the scale of the link function. 67

Figure 2.32. Relative effect of year (on the scale of the response) in the best fixed-effects model (filled points) and corresponding mixed-effects model (open points) for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Points indicate the estimated coefficient for each year relative to the first year, which equals 1. Open points that are not visible indicate identical effects. Note that years with no sightings are not shown. 68

Figure 3.1. Map of the study area (enclosed by solid grey lines). The dashed line indicates the division between the ranges of hypothetical northern and southern subpopulations. 83

Figure 3.2. Marginal posterior probability distributions of the estimated parameters (Table 3.5) of the density-independent model of a single population (Scenario 1, Table 3.6). Plots are histograms of a sample of 10,000 parameter values from the joint posterior. All marginal prior probability distributions were uniform. 107

Figure 3.3. Observed (points) and predicted (lines) sexual maturity ogive for the density-independent model of a single population (Scenario 1, Table 3.6). Solid line indicates median values from the posterior sample and dashed lines represent the 95% interval of values from the posterior sample. The x-axis represents the mid-points of the indicated ages. 108

Figure 3.4. Observed pregnancy rate and predicted birth rate for the density-independent model of a single population (Scenario 1, Table 3.6). The boxplot on the left represents the distribution of observed pregnancy rates across years during the study period (point represents the overall pooled pregnancy rate). The data point and dashed line on the right represent the median and 95% interval of predicted values for birth rate (male and female calves) from the posterior sample, respectively. 109

Figure 3.5. Observed (points) and predicted (lines) age structure of natural and bycatch mortality for the density-independent model of a single population (Scenario 1, Table 3.6). Observed values represent overall proportions (data pooled across years) and predicted values represent average proportions across all years of the study period. Solid line indicates median values from posterior sample and dashed lines represent the 95% interval of values from the posterior sample. Note that the model was fitted to the data from individual years separately (Eqs 3.15 and 3.19), not the pooled data presented in this Figure. 110

Figure 3.6. ‘Observed’ (open circles) and predicted (points and lines) bycatch of males and females in the ten fisheries for the density-independent model of a single population (Scenario 1, Table 3.6). Observed values represent bycatch calculated from the observed bycatch rate in a given year (actual observed bycatch divided by observed effort multiplied by total effort). Points and dashed lines represent the median and 95% interval of predicted values for bycatch (Eq. 3.23) from the posterior sample, respectively. 112

Figure 3.7. Predicted bycatch of males and females in all ten fisheries for the density-independent model of one population (Scenario 1, Table 3.6). Points and dashed lines represent the median and 95% interval of predicted values for bycatch (Eq. 3.23) from the posterior sample, respectively. 113

Figure 3.8. Observed (points) and predicted (lines) total number of males and females during the study period for the density-independent model of a single population (Scenario 1, Table 3.6). The solid line represents median values from the posterior sample and the dashed lines represent the 95% interval of values from the posterior sample. 114

Figure 3.9. Prior and posterior probability distributions for population growth rate in the absence of bycatch for the density-independent model of a single population (Scenario 1, Table 3.6). The distributions for population growth rate were derived from the samples of maturity, birth and natural survival rates from the joint prior and joint posterior. The median posterior population growth rate was 0.99 with a 95% interval of 0.95-1.03..... 115

Figure 3.10. Observed pregnancy rate and predicted birth rate for the density-independent model of a single population with pregnancy data from only ‘healthy’ females (Scenario 2, Table 3.6). The boxplot on the left represents the distribution of observed pregnancy rates across years during the study period (point represents the overall pregnancy rate). The data point and dashed line on the right represent the median and 95% interval of predicted values for birth rate (male and female calves) from the posterior sample, respectively. 116

Figure 3.11. Observed (points) and predicted (lines) age structure of natural mortality for the density-independent model of a single population with pregnancy data from only ‘healthy’ females (Scenario 2, Table 3.6). Observed values represent overall proportions (data pooled across years) and predicted values represent average proportions across all years of the study period. Solid line indicates median values from posterior sample and dashed lines represent the 95% interval of values from the posterior sample. Note that the model was fitted to the data from individual years separately (Eq. 3.15), not the pooled data presented in this Figure. 118

Figure 3.12. Marginal posterior probability distributions of selected estimated parameters (Table 3.5) of the density-dependent population model of a single population (Scenario 6, Table 3.6). Black lines and grey bars are histograms of samples of 10,000 parameter values from the joint prior and posterior, respectively. 120

Figure 3.13. Observed (points) and predicted (lines) total number of males and females during the study period for the density-dependent model of a single population (Scenario 6, Table 3.6). The solid line represents median values from the posterior sample and the dashed lines represent the 95% interval of values from the posterior sample. 121

Figure 3.14. Prior and posterior probability distributions for maximum population growth rate in the absence of bycatch for the density-dependent model of a single population (Scenario 6, Table 3.6). The distributions for population growth rate were derived from the samples of maturity, birth and natural survival rates from the joint prior and joint posterior. The median posterior maximum population growth rate was 1.02 with a 95% interval of 1-1.07. 122

Figure 3.15. Observed pregnancy rate and predicted birth rate for the density-independent model of two subpopulations without dispersal (Scenario 7, Table 3.6). The left and right plots represent the northern and southern North Sea subpopulations, respectively. The boxplots represent the distribution of observed pregnancy rates across years during the study period (point represents the overall pregnancy rate). The data points and dashed lines on the right of each plot represent the median and 95% interval of predicted values for birth rate (male and female calves) from the posterior sample, respectively. 124

Figure 3.16. Predicted bycatch of males and females in all ten fisheries for the density-independent model of two subpopulations (Scenarios 7-9, Table 3.6). The left and right columns represent the northern and southern North Sea subpopulations, respectively. The three rows from top to bottom represent Scenarios 7-9, respectively. Points and dashed lines represent the median and 95% interval of predicted values for bycatch (Eq. 3.23) from the posterior sample, respectively. 125

Figure 3.17. Observed (points) and predicted (lines) total number of males and females during the study period for the density-independent model of two subpopulations (Scenarios 7-9, Table 3.6). The left and right plots represent the northern and southern North Sea subpopulations, respectively. The three rows from top to bottom represent Scenarios 7-9, respectively. The solid lines represent median

values from the posterior sample and the dashed lines represent the 95% interval of values from the posterior sample. 126

Figure 4.1. Performance of three tunings of the PBR and CLA management procedures under the baseline scenario with respect to the conservation objective (long-term population status) and recovery delay. Points represent median results from 100 simulations and error bars represent the 90% interval of simulation outcomes. Population status is defined as population size as a proportion of carrying capacity. The horizontal dashed lines indicate the conservation objective: population status = 0.80. Recovery delay is defined as the delay in recovery of a population to 80% of carrying capacity relative to a scenario without bycatch. 175

Figure 4.2. Trajectories of population status and bycatch (as proportion of population size) for three tunings of the PBR and CLA management procedures under the baseline scenario. Population status is defined as population size as a proportion of carrying capacity. Results are shown for two initial population statuses: 0.10 (left column) and 0.99 (right column). Solid lines represent median results from 100 simulations and dotted lines represent the 90% interval of simulation outcomes. The horizontal dashed lines indicate the conservation objective (population status = 0.80). 176

Figure 4.3. Final population status versus survey precision in simulation trials of the first tuning of the PBR and CLA management procedures. Results are shown for unbiased and biased estimates of survey CVs; biased estimates were half the true CV. Initial population status was 0.80 and all other parameters were set to their baseline values (Table 4.1). Points represent median results from 100 simulations and error bars represent the 90% interval of simulation outcomes. The horizontal dashed lines indicate the conservation objective: population status = 0.80. 179

Figure 4.4. Trajectories of population status and bycatch in a simulation trial of the first tuning of the CLA management procedure where no time-series of historical bycatch was input to the procedure. Initial population status was 0.30, survey CVs were 0.10 (unbiased) and all other parameters were set to their baseline values (Table 4.1). Solid lines represent median results from 100 simulations and dotted lines

represent the 90% interval of simulation outcomes. The dashed line indicates the conservation objective (population status = 0.80). 183

Figure 4.5. Average annual bycatch limit variability versus survey precision in simulation trials of the first tuning of the PBR and CLA management procedures. Results are shown for unbiased and biased estimates of survey CVs; biased estimates were half the true CV. Initial population status was 0.80 and all other parameters were set to their baseline values (Table 4.1). Points represent median results from 100 simulations and error bars represent the 90% interval of simulation outcomes. 185

Figure 4.6. Trajectories of population status (population size as proportion of carrying capacity) and bycatch (as proportion of population size) under the first tuning of the PBR procedure in hypothetical multi-subpopulation simulation Scenarios A-C. Solid lines represent median results from 1000 simulations and dotted lines represent the 90% interval of simulation outcomes. The dashed lines indicate the conservation objective (median population status = 0.80). In Scenario A the subpopulations were managed with two separate management areas whose boundaries corresponded to the ranges of the subpopulations. In Scenario B the subpopulations were managed with one management area encompassing the ranges of both subpopulations, but the second subpopulation was twice as vulnerable to bycatch as the first subpopulation. Scenario C was identical to Scenario B with the exception that each subpopulation had a dispersal rate of 5% per year. 186

Figure 4.7. Trajectories of population status (population size as proportion of carrying capacity) and bycatch (as proportion of population size) under the first tuning of the CLA procedure in hypothetical multi-subpopulation simulation Scenarios A-C. Solid lines represent median results from 1000 simulations and dotted lines represent the 90% interval of simulation outcomes. Dashed lines indicate the conservation objective (median population status = 0.80). In Scenario A the subpopulations were managed with two separate management areas whose boundaries corresponded to the ranges of the subpopulations. In Scenario B the subpopulations were managed with one management area encompassing the ranges of both subpopulations, but the second subpopulation was twice as vulnerable to bycatch as the first subpopulation. Scenario C was identical to Scenario B with the exception that each subpopulation had a dispersal rate of 5% per year. 187

Figure 4.8. Trajectories of population status and bycatch (as proportion of population size) under three tunings of the PBR and CLA management procedures conditioned on the results of the integrated population dynamics model (Chapter 3, Scenario 6). Parameters common to the integrated and operating models were set according to the joint posterior probability distribution; other parameters were set to their baseline values (Table 4.1). Solid lines represent median results from 10,000 simulations and dotted lines represent the 90% interval of simulation outcomes. The dashed line indicates the conservation objective (population status = 0.80). 190

Abstract

Incidental catch, or bycatch, of harbour porpoise (*Phocoena phocoena*) in fishing operations is an international conservation issue. The main objective of this thesis was to develop methods for determining the impact of bycatch on the state and dynamics of porpoise populations and for calculating bycatch limits that will achieve conservation objectives in the future. I applied these methods to the North Sea as a case study.

First, I analysed sighting rates of harbour porpoise on seabird surveys in the North Sea during 1980-2003 to determine whether these data could provide informative time-series of relative abundance. Some general patterns and trends in sighting rates were consistent with previous studies. However, the standardised indices of abundance were relatively imprecise and thus have limited value for a monitoring framework that relies on statistical detection of trends.

Second, I used a population model to integrate available data on harbour porpoise in the North Sea and to assess the dynamics of the population during 1987-2005. There was a high probability that bycatch resulted in a decrease in abundance. The estimated life history parameters suggested a limited scope for population growth even in the absence of bycatch. The model and data were not informative about maximum population growth rate or carrying capacity. The model suggested that dispersal was the most plausible explanation for observed changes in distribution within the North Sea.

Third, I considered management procedures for calculating bycatch limits. I performed simulations to compare the behaviour of the procedures, to tune the procedures to specific conservation objectives and to test the robustness of the procedures to a range of uncertainties regarding population dynamics and structure, the environment, observation and implementation. Preliminary annual bycatch limits for harbour porpoise in the North Sea ranged from 187-1685 depending on the procedure, tuning and management areas used.

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Chapter 1: General Introduction

Bycatch, harbour porpoise and the North Sea

Human activity has greatly affected the state of the world's oceans both directly (e.g., pollution; Islam and Tanaka 2004) and indirectly (e.g., global warming; Levitus et al. 2000). One activity in particular, the harvest of fish, has had a range of effects on marine ecosystems including drastic reductions in harvested populations and biodiversity, and changes in habitat and trophic structure (Hutchings and Myers 1994, Pauly et al. 1998, Jackson et al. 2001, Hilborn et al. 2003, Myers and Worm 2003, Worm et al. 2006). The breadth of impacts on marine ecosystems has brought about recognition that all aspects of an ecosystem, including unharvested species, must be considered when managing activities such as fishing (Browman and Stergiou 2004, Marasco et al. 2007). One of the greatest impacts of fisheries on non-target marine wildlife is incidental catch or bycatch (Hall et al. 2000). A diverse range of species including reptiles, birds and mammals are subject to entrapment and entanglement in fishing operations and many of these events result in the death of individuals (Tasker et al. 2000, Lewison and Crowder 2007, Read 2008).

Mammals are an integral part of many marine ecosystems (Bowen 1997). Populations of marine mammals have been affected by a range of human activities resulting in loss and degradation of habitat, large declines in abundance, and even the extinction of species (Harwood 2001, Baker and Clapham 2004, Turvey and Risley 2006). Fisheries have impacted marine mammal populations both indirectly through competition for shared resources (DeMaster et al. 2001) and directly through bycatch (Read 2008). Read et al. (2006) estimated that hundreds of thousands of marine mammals were bycaught every year around the world during the early 1990s. From a conservation standpoint, the major challenge is to ensure that this bycatch is not impairing the ability of these populations to maintain themselves over time. To meet this challenge requires an understanding of the impact of this bycatch on the size and dynamics of these populations (Lewison et al. 2004).

The North Sea provides a good example of the impacts of human activities on marine ecosystems including the bycatch of marine mammals in fisheries. The North Sea is a relatively shallow body of water over the continental shelf of Northwest Europe. The

North Sea is bordered by industrialised, densely populated countries and thus is affected by numerous human activities including agriculture on surrounding lands, shipping, exploration and extraction of non-renewable energy resources (e.g., oil and gas), renewable energy generation (e.g., tidal and wind power), mariculture, and fisheries (OSPAR Commission 2000). The Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR Convention) is “the current legal instrument guiding international cooperation on the protection of the marine environment of the North-East Atlantic” (<http://www.ospar.org>). The OSPAR Commission has ranked the impacts of fisheries on the North Sea ecosystem among the highest impacts of any human activity (OSPAR Commission 2000). The specific impacts of concern are the removal of target species, alteration of the seabed and mortality of non-target species (bycatch).

Fisheries in the North Sea have resulted in the depletion of several harvested stocks during the past 100 years including mackerel *Scomber scombrus*, herring *Clupea harengus* and cod *Gadus morhua* (Hislop 1996). This removal of target species has altered the structure and function of trophic interactions in the North Sea ecosystem (e.g., increased production of benthic crustaceans because of decreased predation; Heath 2005) although effects on non-target fish species might have been small (Greenstreet and Hall 1996). It is important to note that fisheries were not solely responsible for past changes in North Sea fish assemblages. The environment has also had strong effects on the North Sea ecosystem where trophic interactions are governed by a complex mix of bottom-up and top-down control (Clark and Frid 2001, Heath 2005, Frederiksen et al. 2007). For example, there have been changes in the vertical and latitudinal distributions of fish during the past few decades as a result of warming water temperatures (Beare et al. 2004, Dulvy et al. 2008).

A range of marine wildlife is bycaught in North Sea fisheries including seabirds, seals and small cetaceans (Dunn 1994, Murray et al. 1994, Couperus 1997, ICES 2001). Of these species, the bycatch of harbour porpoise (*Phocoena phocoena* Linnaeus 1758) is the best documented. The harbour porpoise is a widely-distributed small cetacean species found primarily in temperate coastal and shelf waters of the Northern Hemisphere (Gaskin 1984). Throughout their range harbour porpoise are bycaught in fishing gear especially gillnets and driftnets but also towed gear and fish traps (Read

et al. 1993, Stacey et al. 1997, Stenson 2003, Benjamins 2006, Lesage et al. 2006). Several hundred thousand harbour porpoise inhabit European waters (Hammond et al. 2002, SCANS-II 2008) and bycatch has been documented in fisheries of most countries bordering these waters including Denmark, France, Germany, Ireland, the Netherlands, Norway, Poland, Spain, Sweden and the UK (Berggren 1994, Bjørge and Øien 1995, Tregenza et al. 1997, Commission of the European Communities 2002, Kock and Flores 2003, Skóra and Kuklik 2003, Vinther and Larsen 2004, Leopold and Camphuysen 2006, IWC 2007b). Thousands of porpoise were estimated to be bycaught each year in Danish fisheries in the North Sea alone during the 1990s (Vinther and Larsen 2004).

The bycatch of harbour porpoise in the North Sea has generated much public attention and conservation concern. Under the OSPAR Convention a set of Ecological Quality Objectives (EcoQOs) has been developed for the North Sea as part of an integrated, ecosystem approach to management and conservation (OSPAR Commission 2006, Tasker 2006). One of the ten advanced EcoQOs relates solely to harbour porpoise bycatch: to reduce annual bycatch to a level below 1.7% of the best population estimate. This objective was derived from an objective set under another European conservation initiative, the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS 2000). ASCOBANS' draft conservation plan for harbour porpoise in the North Sea lists bycatch as potentially one of the greatest threats and assigns the highest priority to research and conservation action on this issue (Reijnders et al. 2008). The harbour porpoise is listed under Annex II of the European Community (EC) Habitats Directive whose objective is to ensure biodiversity by requiring member states to take measures to "maintain or restore, at favourable conservation status, natural habitats and species of wild fauna and flora of Community interest" (Council of the European Communities 1992). One of the defined criteria for favourable conservation status is that "population dynamics data on the species concerned indicate that it is maintaining itself on a long-term basis as a viable component of its natural habitat". Thus, member states of the EC are obliged to evaluate the effect of bycatch on harbour porpoise populations in their waters.

Despite the conservation concern generated by the bycatch of harbour porpoise in European waters, a comprehensive assessment of the impact of this bycatch on the

state and dynamics of porpoise populations has not been undertaken. Furthermore, there is a need for a robust management framework that can be used to set limits to bycatch that will ensure that conservation objectives are achieved in the future (IWC 2000, Reijnders et al. 2008). The main objectives of my thesis were to develop methods for: 1) determining the impact of bycatch on the state and dynamics of harbour porpoise populations, and 2) calculating bycatch limits that will achieve conservation objectives in the future. I used the North Sea as a case study. Thus, a third objective of my thesis was to apply the methods developed to determine the impact of historical bycatch on harbour porpoise populations in the North Sea, and to provide the means to calculate bycatch limits that can be implemented for the North Sea in the future to achieve specified conservation objectives.

Estimating the impact of bycatch and calculating appropriate limits

Direct anthropogenic removal of animals from wild populations has always been a major focus of wildlife management and conservation, particularly the level of mortality that will achieve management and conservation objectives. For example, the core focus of harvest management is the number of animals that should be harvested to achieve a desired balance between social, economic and conservation objectives (Skalski et al. 2005). In the case of bycatch there is often no social or economic value derived directly from the bycaught individuals, but there are implicit trade-offs between conservation and the socio-economic benefits derived from the fisheries. If conservation were the only objective then the best action would be to close all of the fisheries in which bycatch occurs. Thus, the process for determining appropriate harvest levels and bycatch limits is very similar. Indeed, it has been suggested that conservation and harvest management should really be considered together as part of the science of population management (Shea and NCEAS Working Group on Population Management 1998).

The most direct method for determining whether a population is maintaining itself on a long-term basis in the face of anthropogenic removals is to simply monitor the size of that population over time. Time-series of abundance estimates can be used to estimate trend in population size and predict future population status and probability of extinction (population viability analysis; Dennis et al. 1991, Winship and Trites 2006). Most monitoring programmes are focused on the detection of trends from

count data (Marsh and Trenham 2008). Population trend is commonly one of the criteria used to classify the conservation status of populations under national and international conservation schemes (e.g., IUCN 2001). The EC Habitats Directive requires member states to undertake surveillance monitoring of the conservation status of listed species (Council of the European Communities 1992). One of the criteria defining ‘unfavourable-bad’ conservation status of a population under the Directive is a decline of more than 1% per year over a reference timeframe (European Commission 2006).

In practice, monitoring population size and estimating population trend from such data are not always straightforward. Different sampling designs and different methods of analysis can result in different estimates of trend and different statistical power to detect trends (Thomas 1996, Katzner et al. 2007, Seavy and Reynolds 2007, Blanchard et al. 2008). The frequency and precision of abundance estimates are often too low to provide the statistical power necessary to detect even precipitous declines in abundance in the medium term (10-20 years), especially for marine mammals (Taylor et al. 2007). Delay in the detection of a trend leads to a delay in management action and could result in undesirable risk (Thompson et al. 2000). Most importantly, surveillance monitoring neither elucidates the cause of a decline nor provides information on actions that could be taken to reverse a decline (Nichols and Williams 2006). A decline in a population subject to bycatch is not necessarily attributable to the bycatch. Simple projection of population trend into the future ignores the potential of management actions to alter that trend (Boyce 1992). Thus, monitoring trends in population size alone is not a good approach for estimating the impact of bycatch on a population or determining conservative limits to bycatch.

A useful framework for managing removals takes information about the population as input and calculates a target level of removals or a limit to removals that will achieve the desired management and conservation objectives. One of the simplest such approaches is to compare a current estimate of removals with a current estimate of abundance to calculate an overall removal mortality rate. This removal mortality rate can then be compared to a set objective that is deemed conservative. ASCOBANS has specified exactly such an objective for harbour porpoise bycatch in European waters, 1.7% (ASCOBANS 2000). This number was derived from a simple, deterministic

population model as the mortality rate that would result in the population equilibrating to ASCOBANS' interim conservation objective of 80% of carrying capacity (IWC 2000). The advantage of this approach to managing bycatch is its simplicity. The only information that is required is a single estimate of bycatch and a single estimate of abundance. The calculations are simple and can be easily explained and understood by a wide audience including scientists, managers and other stakeholders. The disadvantages of this approach are that it fails to incorporate other information about the population and that it does not explicitly account for possible errors in the estimates of bycatch and abundance or for uncertainty about the mortality rate that will achieve the conservation objective (i.e., uncertainty about population dynamics).

Biological systems are extremely complex and variable and our knowledge of the states and dynamics of these systems is far from perfect. Estimates of the size of biological populations and estimates of anthropogenic removals from these populations are often imprecise and biased. Managing removals from biological populations to achieve point estimates of sustainable removal rates entails an undesirable level of risk with respect to sustainability because of large uncertainties about population dynamics (Larkin 1977). A more conservative approach is to treat mortality rate objectives as upper limits rather than targets (Mace 2001, Punt and Smith 2001). In the case of bycatch, a mortality rate objective represents an upper limit by design because ideally bycatch would be eliminated (ASCOBANS 2000). Nevertheless, mortality rate limits are still subject to uncertainty about population dynamics. Thus, a simple comparison of point estimates of abundance, bycatch and a bycatch mortality rate limit is not a good approach to ensuring that conservation objectives will be met. A better approach is to account for uncertainty in these estimates when comparing them, which allows for inference about the probability that bycatch is exceeding a conservative level.

Several studies have compared estimates of bycatch, abundance and bycatch mortality rate to evaluate the sustainability of bycatch of marine mammals including harbour porpoise (Woodley and Read 1991, Woodley 1993, Caswell et al. 1998, Dans et al. 2003, Underwood et al. 2008). Monte Carlo simulation techniques and scenario analysis were used to translate uncertainty in estimates into uncertainty about the sustainability of bycatch (Woodley and Read 1991, Caswell et al. 1998). The USA

Government has developed a generic framework for managing anthropogenic removals from marine mammal populations whereby an estimate of removals is compared to a mortality limit termed Potential Biological Removal (PBR; Wade 1998). The PBR framework was designed with the objective of maintaining populations at their optimum sustainable population size which is defined as greater than or equal to their maximum net productivity level (Gerrodette and DeMaster 1990). PBR is calculated as a fraction of a minimum estimate of abundance rather than a point estimate, and an adjustable recovery factor is applied to account for uncertainty in estimates of removals and population dynamics (maximum population growth rate).

Even when uncertainty is accounted for, a simple comparison of current removals and current abundance is limited in that it does not incorporate other information that might be available about the population. Furthermore, such a comparison does not allow explicit prediction about the effect of removals on the future state and dynamics of the population. A more informative and explicit approach is to combine available information about removals and the population in a simulation model. A population model ensures mathematical consistency between inferences about removals and the state and dynamics of the population, and a population model can be used to simulate the past, present and future state and dynamics of the population (Getz and Haight 1989). Many population simulation models have been developed to assess the impact of bycatch on the conservation status of marine wildlife including harbour porpoise (Reijnders 1992, Mangel 1993, Barlow and Hanan 1995, Slooten et al. 2000, Burkhart and Slooten 2003, Lewison and Crowder 2003, Goldsworthy and Page 2007, Underwood et al. 2008). In most of these studies, bycatch, population size and population growth rate were estimated independently. For example, population growth rate was often derived from estimates of survival and reproductive rates based on life history data (Slooten et al. 2000, Lewison and Crowder 2003). Bycatch estimates were treated as input to the simulation models. In all cases, the estimates of bycatch, population size and population growth rate were uncertain. Most studies accounted for this uncertainty using Monte Carlo simulation techniques and scenario analysis (Slooten et al. 2000, Lewison and Crowder 2003).

An elegant approach to assessing the impact of removals on the dynamics of a population is to statistically fit a population model to available data. Embedding a population model in statistical inference allows appropriate representation of uncertainty in estimates of the state and dynamics of the population (Hilborn and Mangel 1997, Buckland et al. 2007). A statistically-fitted population model allows for seamless incorporation of estimation uncertainty into prediction for risk assessment and population viability analysis (Harwood 2000, Wade 2002a, Maunder 2004). Bayesian statistics are particularly useful for characterising uncertainty in population models (Walters and Ludwig 1994, Wade 2000, Harwood and Stokes 2003, Ellison 2004) and have been used frequently in the assessment of fish and marine mammal populations (Punt and Hilborn 1997, McAllister and Kirkwood 1998, Punt and Butterworth 1999, 2002, Wade 2002b, Witting and Born 2005, Brandon and Wade 2006, Skaug et al. 2008). Bayesian population models have also been used to assess the impact of past and future bycatch on populations of marine wildlife (Maunder et al. 2000, Kaplan 2005, Zador et al. 2008). A particularly powerful approach is to fit a population model to a range of types of data—an integrated population dynamics model (Myers et al. 1997, White and Lubow 2002, Goodman 2004, Besbeas and Freeman 2006, Polacheck et al. 2006, Punt 2006, Tinker et al. 2006). Integrated population models can provide more precise estimates of population parameters (e.g., growth rate) by synthesising all of the available information (Schaub et al. 2007, Brooks et al. 2008). Bayesian integrated population dynamics models have been used previously to examine the impact of intentional and unintentional takes of marine wildlife (Alvarez-Flores and Heide-Jørgensen 2004, Hoyle and Maunder 2004). Pout et al. (2001) reported on a preliminary attempt to use a Bayesian integrated population dynamics model to examine the effect of bycatch on harbour porpoise in the North Sea.

Fisheries stock assessment is a good example of a population model-based framework for managing removals from biological populations (Hilborn and Walters 1992, Quinn and Deriso 1999). In the traditional stock assessment approach (Butterworth 2007) statistically-fitted models are used to integrate available data on fish populations and provide a best assessment of key biological parameters (e.g., population size and productivity). Catch limits are then calculated based on some function of these biological parameters (a harvest control rule) or based on simulations of the effects of

different catches on the population in the near future. Estimates of biological parameters have associated measures of uncertainty that allow a precautionary approach to setting catch limits. The International Whaling Commission (IWC) has developed population model-based procedures for setting limits to the catch of baleen whales. The procedure developed for commercial whaling, the Catch Limit Algorithm (CLA), fits a simple population model to time-series of catches and abundance estimates and then sets the catch limit according to a precautionary harvest control rule that operates on the estimated state of the population (Cooke 1999). The IWC has also developed Strike Limit Algorithms for managing aboriginal subsistence harvests (IWC 2007a).

The main benefits of a population model-based approach to managing removals are that it can incorporate all available information about a population resulting in more appropriate removal limits and it allows explicit evaluation of the effect of removals on the state and dynamics of the population. Uncertainty in parameter estimates can be estimated statistically and carried through to prediction. However, despite the conservative elements inherent to this approach, it is still subject to failures arising from incorrect model specification and biased or misleading data. There is no guarantee that a population model-based framework for setting removal limits will perform desirably with respect to management and conservation objectives in the long-term (Butterworth 2007).

To truly evaluate the long-term performance of any framework for setting removal limits one must simulate the entire process over time. This technique is known as management strategy evaluation (MSE) in fisheries science and management (Kell et al. 2007, Rademeyer et al. 2007), and similar approaches have been used for other taxa (e.g., de la Mare 1986, Milner-Gulland et al. 2001, Stephens et al. 2002, Bradshaw et al. 2006). At the core of MSE is a model of the true population, termed the operating model. The operating model simulates the population over time and also simulates observation of the population allowing for random error and bias in the observation process. The simulated observations feed into a management procedure to periodically determine the removal limit. The realized removals can differ from the specified removals to represent random error and bias in the implementation of removal targets and limits (Holt and Peterman 2006). Various criteria related to

removals and the population can be obtained from the simulations to evaluate the performance of the management procedure. The key feature of MSE that mimics reality is that the management procedure does not know the true state of the population; it only has the simulated observations as information.

Through simulation one can examine the performance of alternative management procedures under any scenario imaginable. Simulations should at a minimum address past data, future availability of data, dynamics of the population, dynamics of the removal process, and environmental variability (Rademeyer et al. 2007). An important aspect of population dynamics to consider is the nature and strength of density dependence (Bradshaw et al. 2006, Smith et al. 2008). Environmental variability should include random stochasticity, catastrophes and systematic change (Breen et al. 2003, Kell et al. 2005b). Another important consideration is population structure and the spatial aspect of management, particularly the correspondence between management areas and population boundaries. Simulation testing should be used to examine the performance of different numbers and arrangements of management areas under different hypotheses about population structure and movement (Hammond and Donovan In press). Decisions must be made about plausible ranges of values for the parameters of the operating model and ranges of model structures. One approach is to condition the operating model by statistically fitting it to data. The fitted model then provides estimates for the parameters along with appropriate measures of uncertainty. Conditioned simulations are essentially a hybrid of the traditional stock assessment approach and MSE. The danger with conditioning is that you are effectively limiting the simulation scenarios explored to those consistent with the data, and the data could be misleading as in the case of traditional stock assessment.

Performance criteria related to management and conservation objectives generally fall into three categories: removal-related (e.g., total or average removal), stability-related (e.g., variability in removals over time) and risk-related (e.g., probability of population size declining to some threshold), but there are other possible objectives such as social considerations (Rademeyer et al. 2007). An example of a social objective is the IWC's consideration of subsistence need in the development of Aboriginal Whaling Management Procedures (IWC 2007a). In a bycatch context,

removal-related and stability-related objectives are not directly relevant with respect to the bycatch itself, but are relevant with respect to the fishery assuming that fishing effort is correlated with bycatch. Trade-offs among management and conservation objectives make it difficult to determine the optimal management procedure. The most obvious trade-off is between removal- and risk-related objectives. An ideal management procedure would achieve the optimal balance between these objectives that maximised overall value (Bue et al. 2008). However, even if the different objectives can be translated into a common currency, optimisation is difficult for complex, stochastic systems (Walters and Hilborn 1978, Milner-Gulland 1997, Witting 1999). Decision analysis is an alternative to true optimisation: the best management option is selected from a discrete set of management options based on the expected costs and benefits under each option (Walters and Hilborn 1978, Harwood 2000). In practice, there can be a range of strategies that result in only slightly suboptimal performance (Bue et al. 2008), and these suboptimal strategies can be easier to implement and less prone to failure as a result of incorrect assumptions about removals and population dynamics (Milner-Gulland 1997). A practical approach for a bycatch situation is to develop management procedures that achieve a common risk-related or conservation objective(s), and then evaluate these management procedures on the basis of their performance with respect to fishery-related criteria.

A lot of research has been devoted to the performance of different removal strategies in the context of natural stochasticity and imperfect knowledge about ecological systems. One general conclusion from theoretical and empirical studies of simple systems is that removal strategies with constant removal rates or thresholds below which no removal occurs (constant escapement) perform better with respect to variability in population size, sustainability and total long-term harvest than do strategies with constant removals (Beddington and May 1977, Harwood 1978, Lande et al. 1995, Stephens et al. 2002, Fryxell et al. 2005). By design, strategies with constant removal rates or constant escapement have more variable removals, although constant-rate strategies have less variable effort if catchability is constant. Constant-rate and constant-escapement removal strategies require new information about the population over time and thus qualify as management procedures. New information provides feedback to the management procedure and allows the removal limit to

respond appropriately to changes in the population. Management procedures can be further classified as empirical or model-based (Rademeyer et al. 2007). Empirical management procedures set removals based directly on new data while model-based management procedures use new data to update estimates of the parameters of a population model which are then used to set removals. Empirical management procedures are easier to understand and faster to implement, but tend to lead to more variability in removals over time than model-based management procedures. The PBR management framework is an empirical management procedure and it was developed using an MSE approach (Wade 1998). Model-based management procedures are more complex, but have the potential to learn about the dynamics of the affected population over time (e.g., equilibrium population size, maximum population growth rate) and adjust the removal limits appropriately. The traditional stock assessment approach and the CLA are model-based management procedures and their long-term performance has been evaluated through MSE (Kell et al. 2005a, Schnute and Haigh 2006, Pastoors et al. 2007, Punt and Donovan 2007, Hammond and Donovan In press). Two desirable features of any management procedure are input data and parameters that are easily estimated, and explicit accounting for uncertainty (Taylor et al. 2000).

Model-based management procedures are closed-loop policies that take account of future learning about the system (Walters and Hilborn 1978). Thus, model-based management procedures have the potential to correct initial systematic errors in estimates of biological parameters (e.g., population productivity) and adjust the removal level appropriately. Commonly, model-based management procedures are passive-adaptive whereby the learning process is dictated by natural variability and random errors (Walters and Hilborn 1978). Walters and Hilborn (1978) advocated an active-adaptive approach whereby management actions are deliberate experiments with a dual effect on short-term performance and long-term performance (through the learning process). They pointed out that an active-adaptive approach is especially useful in systems where natural disturbances are not sufficient to create the contrast in states needed for efficient learning through a passive approach. Optimisation of an active-adaptive management approach to a complex, stochastic system is very difficult, partially as a result of trade-offs between the dual effect of management actions, but approximate approaches can be used (Walters and Hilborn 1978, Martell

and Walters 2008). The value of an active-adaptive approach can depend on the time horizon and future discounting rate (Hauser and Possingham 2008).

Data

The development of useful methods of analysis is necessarily linked to the number and types of data that are available for analysis. The harbour porpoise is a relatively well-studied species of small cetacean. Thus, there is a fair amount of information available that is relevant to the dynamics of harbour porpoise populations in the North Sea.

Data on the size of a population are fundamental to an analysis of population dynamics and the impact of bycatch. Surveys provide the most direct estimates of the size or relative size of a population. A variety of platforms have been used to survey harbour porpoise populations including land (Evans et al. 1997), small boats (Williams and Thomas 2007), ships (Hammond et al. 2002), and aircraft (Forney 1999, Scheidat et al. 2004). Typically, the number of visual detections of harbour porpoise at the surface is used to estimate abundance or relative abundance. More recently passive acoustic methods have become popular for estimating relative abundance; towed and stationary hydrophones are used to detect porpoise echolocation clicks (Gillespie et al. 2005, Carstensen et al. 2006, Embling 2007, Verfuß et al. 2007). Visual and acoustic detection rates (e.g., per unit time or distance travelled) can be used as measures of relative abundance, but are not measures of absolute abundance. Line-transect distance-sampling methodology provides a framework for estimating density (Buckland et al. 2001) and has been implemented in visual surveys for harbour porpoise (Palka 1995, Raum-Suryan and Harvey 1998, Forney 1999, Dalheim et al. 2000). However, because harbour porpoise spend much of their time underwater and detecting harbour porpoise at the surface can be challenging, density estimates for harbour porpoise must be corrected for animals missed on the track line in order to derive estimates of absolute abundance (Laake et al. 1997, Hiby and Lovell 1998).

There are two estimates of harbour porpoise abundance for the North Sea, one from 1994 and one from 2005, both from late June/July (Hammond et al. 2002, SCANS-II 2008). These estimates were from ship and aerial surveys and were corrected for

animals missed on the track line and movement in response to ship surveys. The estimates were not significantly different from each other (although power to detect such a difference was low), however, there was a significant shift in distribution such that there were relatively more harbour porpoise in the southern North Sea in 2005 than in 1994 (SCANS-II 2008). These estimates of absolute abundance are vital to an analysis of the impact of bycatch and the management of future bycatch.

Unfortunately, there are only two estimates 11 years apart because of the financial cost and logistical difficulty of obtaining these estimates. There are several other estimates of harbour porpoise abundance for parts of the North Sea and adjacent waters during the past 20 years (Heide-Jørgensen et al. 1993, Berggren and Arrhenius 1995, Bjørge and Øien 1995, Siebert et al. 2006, Thomsen et al. 2006). However, these surveys only covered part of the study area, and most of these estimates were not corrected for porpoise missed on the track line.

Data on the relative abundance of harbour porpoise in the North Sea could augment the few absolute abundance data. Relative abundance data are generally cheaper to obtain and easier to collect from platforms of opportunity such as passenger ferries, whale-watching boats, industrial vessels (e.g., oil rig supply ships) and other scientific vessels (Evans and Hammond 2004, SCANS-II 2008). Time-series of relative abundance data can provide information on trends in population size. For example, a >30-year time-series of shore-based sighting rates has indicated an increase in the abundance of harbour porpoise along the coast of the Netherlands during the past 20 years (Camphuysen 2004). The European Seabirds at Sea (ESAS) database is a potential source of relative abundance data for the North Sea as a whole (Northridge et al. 1995). The ESAS database contains information on marine mammal sightings (including harbour porpoise) during extensive seabird surveys in the North Sea and European Atlantic since 1980. These data were made available for this thesis.

The rate of change in the size of a population over time is a function of immigration, emigration, reproduction and mortality. Thus, data on the life history of a species are also useful to an analysis of population dynamics and the impact of bycatch.

Important life history features include longevity, age-specific survival rates, age at sexual maturity and birth rate.

The life history of harbour porpoise has been particularly well-studied in the North Atlantic Ocean (Lockyer 2003). Life history data have come from the post-mortem examination of specimens that were directly caught, bycaught or stranded onshore. The ages of harbour porpoise are determined from their teeth (Bjørge et al. 1995, Lockyer 1995c). Dentine and cementum are deposited in layers giving rise to growth layer groups that represent years of life. These growth layer groups are counted from decalcified, stained sections of teeth. The oldest age recorded for male and female harbour porpoise in the North Atlantic is 24 years (Lockyer 1995b, Lockyer 2003). However, the frequency distributions of ages in samples of stranded and bycaught porpoise show a rapid decrease in numbers with age so that only fractions of these samples are older than 10 years (Lockyer 1995b, Read and Hohn 1995, Lockyer et al. 2001, Lockyer and Kinze 2003, Ólafsdóttir et al. 2003). This age structure suggests that the overall survival rate is relatively low. However, it is important to recognize that these samples only represent animals that were directly caught or bycaught or died in a fishing operation or naturally and then subsequently stranded. Age-specific differences in vulnerability to catch/bycatch or in the propensity of a carcass to strand would bias simple inferences about survival rates based on these data. Unfortunately, there are no direct data on the survival rates of wild harbour porpoise (e.g., mark-recapture studies). Several previous studies have modelled harbour porpoise survivorship based on other mammal species (Barlow and Boveng 1991, Woodley and Read 1991, Caswell et al. 1998).

Post-mortem examinations of harbour porpoise have also provided information on reproductive parameters including age at sexual maturity and pregnancy rate. Sexual maturity in females is established through the presence of corpora albicantia or corpora lutea in the ovaries, which indicates ovulation (Read 1990a). Sexual maturity in males is established through histological examination of the testes to determine whether active spermatogenesis is occurring (Sørensen and Kinze 1994, Read and Hohn 1995). Most male and female harbour porpoise in the North Atlantic reach sexual maturity when they are 3-4 years old (Read 1990a, Read and Gaskin 1990, Sørensen and Kinze 1994, Lockyer 1995a, Read and Hohn 1995, Lockyer et al. 2001, Lockyer and Kinze 2003, Ólafsdóttir et al. 2003, Learmonth 2006). Female harbour porpoise in the North Atlantic have a seasonal reproductive cycle with calving and mating during the late spring and summer and a gestation period of 10-11 months

(Read 1990b, Sørensen and Kinze 1994, Börjesson and Read 2003, Lockyer 2003, Learmonth 2006). Pregnancy is usually established directly by the presence of a foetus in the uterus, but the presence of a corpus luteum has also been used to establish pregnancy, particularly in early gestation when the foetus is small and could be missed during examination (Read 1990a, Sørensen and Kinze 1994). Estimated pregnancy rates of harbour porpoise in the North Atlantic are highly variable ranging from as low as 42% to over 90% (Read 1990a, Read and Gaskin 1990, Sørensen and Kinze 1994, Read and Hohn 1995, Ólafsdóttir et al. 2003, Learmonth 2006).

Two of the largest datasets on the life history of harbour porpoise in the North Sea are those held by the Institute of Zoology (UK) and the National Institute of Aquatic Resources (Denmark). These datasets contain information on the age, sexual maturity and reproductive status of hundreds of directly-caught, bycaught and stranded specimens during the past several decades. These data were made available for this thesis.

An analysis of the impact of bycatch on a population requires not only information about population size and life history but also information about the bycatch itself. Specifically, it is desirable to know the number of animals that are bycaught and the composition of the animals that are bycaught (e.g., age structure).

It is generally not possible to determine exactly how many harbour porpoise die as a result of bycatch. Many stranded harbour porpoise carcasses exhibit visible marks indicative of entanglement in nets (Cox et al. 1998, Jepson 2003, Leeney et al. in press). The number of such carcasses provides a minimum estimate of the number of animals dying as a result of bycatch, but this estimate does not include carcasses that fail to strand or that are simply not found. A more direct method of estimating the number of animals that are bycaught is to monitor the fisheries. Monitoring can be indirect through interviews, surveys and voluntary reporting by fishermen (Kinze 1994, Bjørge and Øien 1995, Hall et al. 2002, Lesage et al. 2006, Read 2008) or fisheries can be monitored directly through the placement of observers on fishing vessels (e.g., Tregenza et al. 1997, Vinther 1999). The latter produces the most reliable estimates of bycatch (Donovan and Bjørge 1995). However, logistical and financial restrictions often mean that observer programmes only cover a portion of total fishing effort. For example, it is often not possible to place observers on small

fishing vessels because of limited space. The total number of porpoise bycaught must then be extrapolated from the number of porpoise bycaught per unit of observed fishing effort and the total fishing effort. In the case of gillnetting, the best measure of fishing effort from which to extrapolate bycatch is the total length of net set and the duration that the net was in the water (Donovan and Bjørge 1995). However, these measures of fishing effort are not always available for entire fleets so other measures of effort are commonly used including days at sea and fish landings (Vinther and Larsen 2004).

As discussed earlier, bycatch of harbour porpoise has been documented in set-net fisheries of many countries bordering the North Sea. Two of these countries with large fisheries, the UK and Denmark, implemented observer programmes during the 1990s to estimate bycatch rates and extrapolate total bycatch in many of their fisheries (Vinther 1999, Northridge et al. 2007). These data were made available for this thesis. Furthermore, data on the ages of bycaught porpoise and stranded porpoise that were diagnosed as having died from bycatch were available from the life history datasets mentioned previously.

The final type of information needed to determine the impact of bycatch on a population is population structure. Conservation is generally aimed at maintaining unique genetic, ecological and morphological units, or management units, throughout a species range (Taylor and Dizon 1999, Fraser and Bernatchez 2001). Assessment of the impact of bycatch and management of future bycatch should be at the resolution of these management units. Thus, it is important to understand genetic, ecological and morphological differentiation within a population. Furthermore, it is important to understand the rate of dispersal of animals between units.

The genetics of harbour porpoise populations have been studied throughout the species' range. Significant genetic differentiation has been documented between harbour porpoise populations in different ocean basins and between populations on different sides of ocean basins (Rosel et al. 1995, Wang et al. 1996, Rosel et al. 1999b, Tolley et al. 2001, Viaud-Martínez et al. 2007). Genetic differentiation has also been found within regions including the Northeast Pacific, Northwest Atlantic and Northeast Atlantic (Andersen 1993, Wang et al. 1996, Andersen et al. 1997, Wang and Berggren 1997, Rosel et al. 1999a, Chivers et al. 2002, Duke 2003). There

even appears to be genetic differentiation between groups of porpoise in different parts of the North Sea including north-south differences and east-west differences (Walton 1997, Tolley et al. 1999, Andersen et al. 2001). Some of the most recent genetic studies of harbour porpoise in the Northeast Atlantic have suggested that an isolation-by-distance model might be the most accurate representation of harbour porpoise population structure in this region, rather than a set of discrete subpopulations (Tolley and Rosel 2006, Fontaine et al. 2007a).

Phenotypic differences have also been observed between harbour porpoise populations at various scales. Skull morphology is significantly different between populations of harbour porpoise across regions (Amano and Miyazaki 1992, Viaud-Martínez et al. 2007) and within regions including the Northeast Atlantic (Kinze 1985, Gao and Gaskin 1996, Börjesson and Berggren 1997, Gao and Gaskin 1998, Tolley 1998). Concentrations of chemical pollutants, trace elements and isotopes in harbour porpoise tissues vary between and within regions suggesting segregation of foraging and limited movement between regions (Kleivane et al. 1995, Berrow et al. 1998, Berggren et al. 1999, Westgate and Tolley 1999, Tolley and Heldal 2002, Das et al. 2004, Van de Vijver et al. 2004, Fontaine et al. 2007b). Lahaye et al. (2007) found elevated concentrations of cadmium in harbour porpoise from the northern North Sea (Scotland) and elevated levels of zinc in porpoise from the southern North Sea (Netherlands), and suggested that these differences might reflect long-term segregation of animals between these areas.

There are few direct data on movements of harbour porpoise. Coordinated seasonal movements of harbour porpoise have been suggested for some areas (Read et al. 1993). There was a large historical migration of porpoise from the Baltic Sea into the North Sea during the winter prior to the mid-20th century but this migration, if it still occurs, is only a fraction of its historical size because of a decrease in population size, which was at least partially a result of historical hunting (Andersen 1982). There is evidence of current seasonal movements of harbour porpoise in other parts of the North Sea (e.g., higher numbers in Dutch coastal waters during winter and spring; Camphuysen 2004). Satellite telemetry has provided some information about the nature of individual harbour porpoise movements and has indicated that animals can range widely moving hundreds of kilometres in a matter of weeks (Read and Westgate

1997). Movements of individual harbour porpoise in the North, Kattegat and Skagerrak Seas and inner Danish waters indicate that population structure may exist within that area, although some long-range movements were observed (Teilmann et al. 2004).

Data on population structure are not analyzed in this thesis, but the analyses presented are set in the context of alternative hypotheses about the population structure of harbour porpoise in the North Sea.

Thesis structure

As outlined earlier, the main objectives of my thesis were to 1) develop methods for determining the impact of bycatch on the state and dynamics of harbour porpoise populations, 2) develop methods for calculating limits to bycatch that will achieve conservation objectives in the future, and 3) apply these methods to determine the impact of historical bycatch on harbour porpoise populations in the North Sea and provide the means to calculate bycatch limits that can be implemented for the North Sea in the future to achieve specified conservation objectives.

Chapter 2 of my thesis presents an analysis of data from the ESAS database that could potentially provide information about the relative abundance of harbour porpoise in the North Sea over time. This information could be useful to the methods developed later in my thesis. Statistical models were fitted to data on sighting rates to derive standardised time-series of relative abundance for harbour porpoise in the North Sea during the past 25 years. Observed trends in relative abundance were compared to existing information on the abundance and distribution of harbour porpoise in the North Sea. I examined the precision of the estimates of relative abundance to assess the level of information that they would provide to analyses of the impact of bycatch.

Chapter 3 of my thesis presents an integrated population dynamics model for harbour porpoise. I used the model to assess the population dynamics and conservation status of harbour porpoise in the North Sea and the impact of previous bycatch. The model was fitted to concurrent data on bycatch rate, abundance and life history to derive estimates of bycatch, population growth rate (with and without bycatch) and carrying capacity with appropriate estimates of uncertainty. The model allowed me to evaluate the consistency of the different datasets and to examine the plausibility of different

hypotheses regarding the dynamics and structure of harbour porpoise populations in the North Sea.

Chapter 4 of my thesis presents a management framework for setting limits to bycatch of harbour porpoise in the North Sea to achieve specified conservation objectives. I considered the PBR and CLA procedures as candidate management procedures. MSE was used to compare and contrast the behaviour of the two procedures, to tune the procedures so that one would expect to achieve specific conservation objectives in practice, to conduct a set of generic simulation trials to evaluate the robustness of my tunings to a range of biases, stochasticity and uncertainty, and to conduct conditioned simulation trials of the procedures for harbour porpoise in the North Sea using the integrated population dynamics model from Chapter 3. The tuned procedures were used to calculate preliminary bycatch limits for harbour porpoise in the North Sea. An appendix to Chapter 4 is presented as a Portable Document Format (PDF) file named 'Appendix' on the supplementary compact disc included with this thesis.

Chapter 5 presents a general discussion of the methods, results and conclusions presented in Chapters 2-4.

In addition to the material presented in this thesis I have authored two published papers with related subject matter during my thesis research.

In the first of these papers, Winship and Trites (2006) present a population viability analysis for the Steller sea lion in western Alaska, USA. An age-structured population model was fitted to historical count data and then projected into the future to examine the risk of extirpation under several scenarios (e.g., density-independent and density-dependent population dynamics). The results suggested that the risk of extirpation of the Steller sea lion in western Alaska in the next 100 years was low; however, most subpopulations had high probabilities of going extinct if trends observed during the 1990s continued. The analysis highlighted two clusters of contiguous subpopulations that had relatively lower risks of extinction.

In the second paper, Williams et al. (2008) present preliminary limits to anthropogenic mortality of small cetaceans (including harbour porpoise) in coastal waters of British Columbia, Canada. Canada does not have a generic method for determining appropriate removal limits for marine mammal populations. We applied

the PBR approach to recent estimates of abundance and bycatch given the conservation objectives of the USA Marine Mammal Protection Act and ASCOBANS. Estimates of bycatch mortality in 2004 and 2005 exceeded only the most precautionary limits and only for porpoise species.

Chapter 2: Standardised indices of harbour porpoise abundance in the North Sea from European Seabirds at Sea surveys

Introduction

Time-series of data on animal abundance are fundamental to the understanding of the dynamics and management of populations. Uses of such data range from simple estimation of population growth rate to the fitting of complex, integrated models of population dynamics (e.g., Buckland et al. 2004). Data on abundance and removals alone can provide information crucial to the management of populations including the nature of population regulation (Goodman 1988, Brook and Bradshaw 2006) and probability of extinction (Dennis et al. 1991) and can drive harvest management procedures (Cooke 1999).

It is difficult and costly to obtain estimates of absolute abundance for marine animals so indices of abundance are often used to assess population dynamics. For example, fisheries stock assessments often rely on catch-per-unit-effort data from fisheries or scientific surveys (Hilborn and Walters 1992). Monitoring and assessment of marine mammal populations also commonly rely on relative abundance data such as sighting rates or the abundance of some component of the population (Punt and Butterworth 1999, Thomas et al. 2005, Taylor et al. 2007).

While time-series of relative abundance can provide valuable information about population dynamics, it is important to account for the dynamics of the relationship between the index of abundance and absolute abundance (Berkson and DeMaster 1985, Harley et al. 2001, Maunder et al. 2006, Shea et al. 2006). It is also important to account for confounding factors that influence abundance and detectability. For example, catch-per-unit-effort data are generally standardised to control for such effects as fishing vessel, time of year and area when deriving annual indices of abundance (Campbell 2004, Maunder and Punt 2004). Data on the relative abundance of marine mammals are also commonly standardised to account for factors such as sighting conditions, time of year and area (Forney 1999, Buckland and Breiwick 2002, Small et al. 2003). One approach to standardisation is to use generalized linear and additive statistical models (Hastie et al. 2001, Venables and Ripley 2002) to estimate the marginal index of abundance for each year (and its associated

uncertainty) after controlling for the effects of other variables. These statistical models reduce bias and potentially increase the precision of time-series of relative abundance data (Forney 2000). Nevertheless, the statistical power to detect trends from time-series of relative abundance data for marine mammals is often low (Taylor et al. 2007).

Reliable estimates of population size and growth rate are prerequisites for assessing the impact of bycatch on harbour porpoise populations in the European Atlantic and North Sea (Stenson 2003). However, dedicated surveys to estimate the absolute abundance of these populations are costly and occur infrequently (Hammond et al. 2002). Time-series of relative abundance data would complement the few absolute abundance data that exist, and may improve our ability to assess the dynamics of these populations (Evans and Hammond 2004).

The European Seabirds at Sea (ESAS) database contains a large number of data from shipboard visual surveys that have been conducted using a rigorous protocol in European waters over the past 25 years (Tasker et al. 1984). While the primary focus and study design of these surveys were related to seabirds, observers also recorded sightings of marine mammals. The objective of this chapter was to determine whether the sighting rates of harbour porpoise on these surveys might provide useful time-series of relative abundance. Previous studies of cetacean sighting data in the ESAS database have highlighted the complications in interpreting these data because of the use of multiple vessels and observers and the sometimes opportunistic nature of the data collection (Northridge et al. 1995, Bravington et al. 1999, Bravington et al. 2002). For my analysis I focused on harbour porpoise sightings in the North Sea. I extracted seven of the longest, most extensive, and most consistent time-series of survey effort in the North Sea from the ESAS database. I then fitted statistical models to these data to derive annual indices of abundance for harbour porpoise in this region during the past 25 years. I compared the observed trends in relative abundance to existing information on the dynamics of harbour porpoise in the North Sea, and I examined the precision of these indices of abundance to determine the level of information that they would provide to analyses of population dynamics.

Methods

ESAS survey methodology and database

Ship surveys were conducted along transects with several different observation protocols related to the bird species of interest on a given survey (Tasker et al. 1984, Camphuysen et al. 2004). In general, all cetaceans sighted forward of the ship were recorded. Data were recorded in ‘recording periods’ of variable length although the length of the majority of recording periods on a given survey usually fell into one or a few categories (e.g., 10 minutes). Thus, each record in the database corresponded to a single recording period and these were used as the replicates in my statistical analysis.

The species and number of animals in each group of cetaceans sighted during a recording period was recorded. However, there was some question as to whether groups of cetaceans were always recorded separately so I chose to analyse the total number of harbour porpoise sighted during a recording period (the dependent variable). Exact distances and angles to animals were not recorded, however, many records contain categorized data on distance from the track line within the bird strip transect or specify that the animal was outside the transect.

The effort variable associated with each recording period was distance travelled; duration was not in the database. Duration had to be inferred from the start times of sequential recording periods. Records with zero distance were not analysed. Each data record contained additional information about several variables that could potentially influence the sightability of cetaceans including the number of observers (simultaneous, non-independent), use of binoculars, bird observation protocol (‘count type’), bird strip transect width, sea state and visibility. The latter was primarily entered in categories (e.g., poor, good), but was entered as distance for one subset of the data (subset 5; see below). Variables in the database that could potentially have affected the behaviour (and thus sightability) and/or abundance of small cetaceans included year, day of year, time of day (at the start of a recording period), and longitude/latitude (at the mid-point of a recording period). I created a new variable, relative time of daylight, from time of day and used this variable instead of time of day. An algorithm was used to calculate time of sunrise and sunset for a given date and location (Nautical Almanac Office 1990), and relative time of daylight was

calculated so that sunrise was -1 , sunset was 1 , and mid-daylight was 0 . Not all records contained data for all variables.

Vessel speed was not in the database but might affect sighting rate so I calculated the duration of each recording period and then calculated speed from duration and distance. I had to correct many apparent errors in times and days, but the magnitudes of these changes were usually only a few minutes or a single day, respectively. The duration of a given recording period was calculated as the difference between the start time of that recording period and the start time of the following recording period. However, this calculation was not appropriate when there was a break in effort between two subsequent recording periods. Some of the data had position codes that could be used to determine breaks in effort and some of the data had end times for transects that could be used to calculate the duration of the recording period preceding a break. For the remaining data I developed an algorithm to determine breaks in effort and the duration of recording periods preceding breaks.

The main assumptions of the algorithm used to estimate duration were: 1) unless otherwise indicated the maximum duration of a recording period was 31 minutes—a longer interval between the start times of two sequential recording periods indicated a break in effort, 2) a 33% reduction in apparent speed (distance travelled during a recording period divided by the difference between the start time of that recording period and the start time of the next recording period) between consecutive recording periods indicated a break in effort, and 3) unless otherwise indicated speed was constant. When the algorithm determined a break in effort, the duration of the recording period preceding that break was calculated from the distance for that recording period and the speed from the previous recording period. This algorithm was not perfect because of violations of the above assumptions. For example, there were sometimes apparent reductions in speed $>33\%$. When this occurred the algorithm specified a break in effort and the duration of the recording period preceding the break was underestimated while the speed during that recording period was overestimated (speed was assumed to be the same as in the previous recording period). Given that the duration calculation was straightforward for the majority of recording periods, I felt that its accuracy was sufficient to allow me to detect any

strong effects of speed on sighting rate. Data records with estimated speeds >50 km/h were not analysed.

In one subset of the data that I analysed (subset 5) there were many recording periods that were only 1 minute in duration. For these data I developed an algorithm that pooled contiguous recording periods into recording periods with a maximum duration of 10 minutes. Sea state and visibility were averaged and rounded for the pooled recording periods.

The data were extremely heterogeneous with respect to ships and observers. Large numbers of ships and observers were used and there were many instances of partial and complete confounding between ship and/or observer and other variables of interest including year (e.g., different, unique ships and/or observers used in different years). Furthermore, multiple protocols with respect to observer rotation and data recording were apparent in the database. There was usually only one set of data for a given transect, but these data represented one to several observers who either observed simultaneously (non-independently) and/or traded off throughout a day with varying lengths of observation. When there were multiple non-independent observers, only the 'primary' observer's identity code was recorded in the database. There were also cases where multiple observers apparently observed simultaneously but recorded separate, different sightings data, potentially suggesting different areas of focus (e.g., different sides of the ship). Only one subset of the data that I analysed (subset 5) had instances of duplicated effort data (from multiple observers) for a single track. I excluded these duplicated data from my analysis to avoid introducing un-modelled correlation.

Missing and inconsistent vessel and observer codes further complicated interpretation of observer rotation protocols. I had to make many reversible changes to ship and observer codes in order to sort the data and calculate the duration of recording periods. For example, recoding was necessary when two apparently different transects (different locations) had the same ship code and date. In that case, suffixes were added to the ship codes to distinguish the two transects for sorting. Missing vessel and observer codes were replaced with temporary codes. These changes were reversed prior to analysis. The data that I analysed contained very few missing observer and vessel data.

Selected data

To limit confounding between the effects of ships and research design and other variables of interest I extracted seven of the longest, most extensive, and most consistent time-series of survey effort in the North Sea from the ESAS database and analysed each of these subsets separately (Table 2.1). Each data subset represented effort from a single research group. Three subsets were data from a single ship, two subsets were from pairs of ships and the remaining subsets had data from more than two ships (Figs 2.1-2.4). The number of observers in each subset ranged from 9-26 (Figs 2.5-2.11). The span of the time-series ranged from 6-17 years between 1980 and 2003 representing 3-14 years of data. Subsets 5 and 7 contained data from throughout the year, while the other subsets each represented data from 2 months or less during the summer (June-September). Within each subset, the spatial coverage was relatively consistent across years (Figs 2.12-2.18) and together the data covered most of the North Sea (Fig. 2.19). Subset 7 was unique in that the ships used were ferries. Thus, survey effort in this subset was comprised of several relatively long and straight transects, which generally varied in location among years (Fig. 2.18).

Statistical modelling

Variables

My primary objective in analysing the ESAS data was to derive time-series of relative abundance. The number of harbour porpoise sighted per recording period was chosen as the dependent variable, and thus the index of abundance. Statistical models were used to estimate the effect of year on this index after controlling for the effects of other variables. By including explanatory variables that potentially affected the sightability of harbour porpoise, I attempted to restrict the effect of year to reflect differences in abundance rather than sightability.

Table 2.1. Subsets of survey effort in the North Sea from the ESAS database analysed in this study. Latitudes and longitudes represent spatial boundaries that I applied to certain subsets. Date ranges represent the earliest and latest dates of analysed effort across all years. Numbers of ships and observers represent numbers of unique ship and observer codes. Data sources are: 1) Joint Nature Conservation Committee (UK); 2) Instituut voor Bos en Natuur (Netherlands); 3) Royal Netherlands Institute for Sea Research (NIOZ); 4) Institute of Nature Conservation (Belgium); 5) Vogelwarte Helgoland (Germany).

Subset	Area	Dates/Years	# Ships	# Observers	Complications	Source
1	northwest >56°N <2°E	4-31 Jul 1982, 84, 87, 90-92, 97-98	1	12	no sightings in 1990	1
2	west >54°N <3°E	7 Jun-20 Jul 1991, 93-95, 97-99, 2001-03	2	21	no visibility data for 1995; binoculars used in 1995	2,3
3	west >53°N <58.5°N <3°E	31 Aug-30 Sep 1987-94	2	13	no visibility data for 1994; binoculars used in 1994; no sightings in 1987	2,3
4	southwest <3.5°E	18 Aug-30 Sep 1995-2001	1	9		4

Table 2.1 contd.

Subset	Area	Dates/Years	# Ships	# Observers	Complications	Source
5	southeast $\leq 57^{\circ}\text{N}$ $\geq 3^{\circ}\text{E}$	year-round 1990-2003	19	26	pooled recording periods; missing visibility data for many sightings; binoculars used in later years; no sightings in 4 years	5
6	all	1 Aug-30 Sep 1993-94, 98	1	9	no visibility data for 1994; binoculars used in 1994	2,3
7	all	year-round 1980-87	9 (ferries)	20	few long, straight transects; no sightings in 1983	1

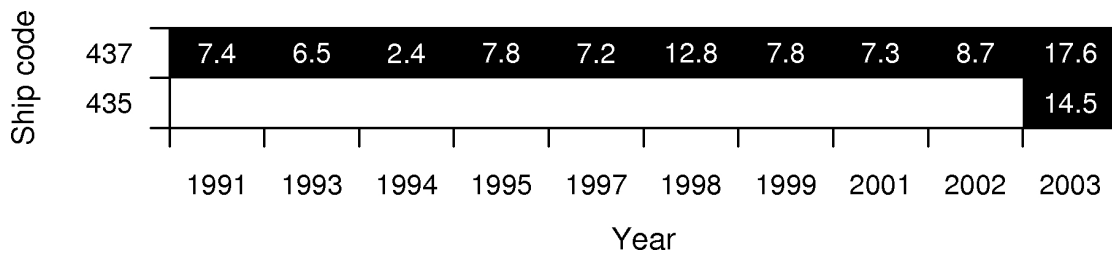


Figure 2.1. Distribution of survey effort among ships for data subset 2 (Table 2.1). Black bars indicate years in which individual ships were used for survey effort. Numbers within the bars indicate the percentage of total effort represented by that ship in that year.

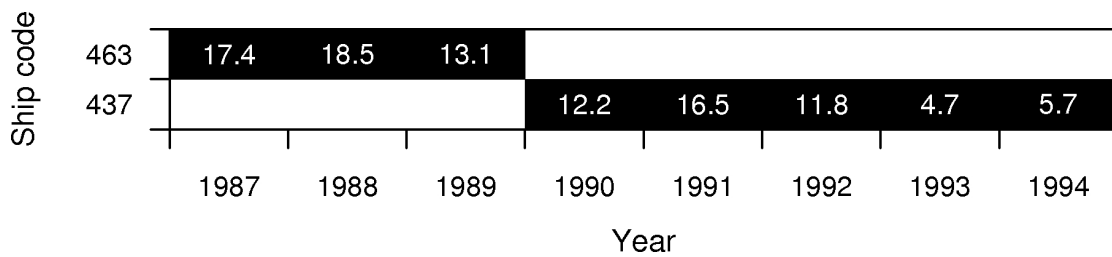


Figure 2.2. Distribution of survey effort among ships for data subset 3 (Table 2.1). Black bars indicate years in which individual ships were used for survey effort. Numbers within the bars indicate the percentage of total effort represented by that ship in that year.

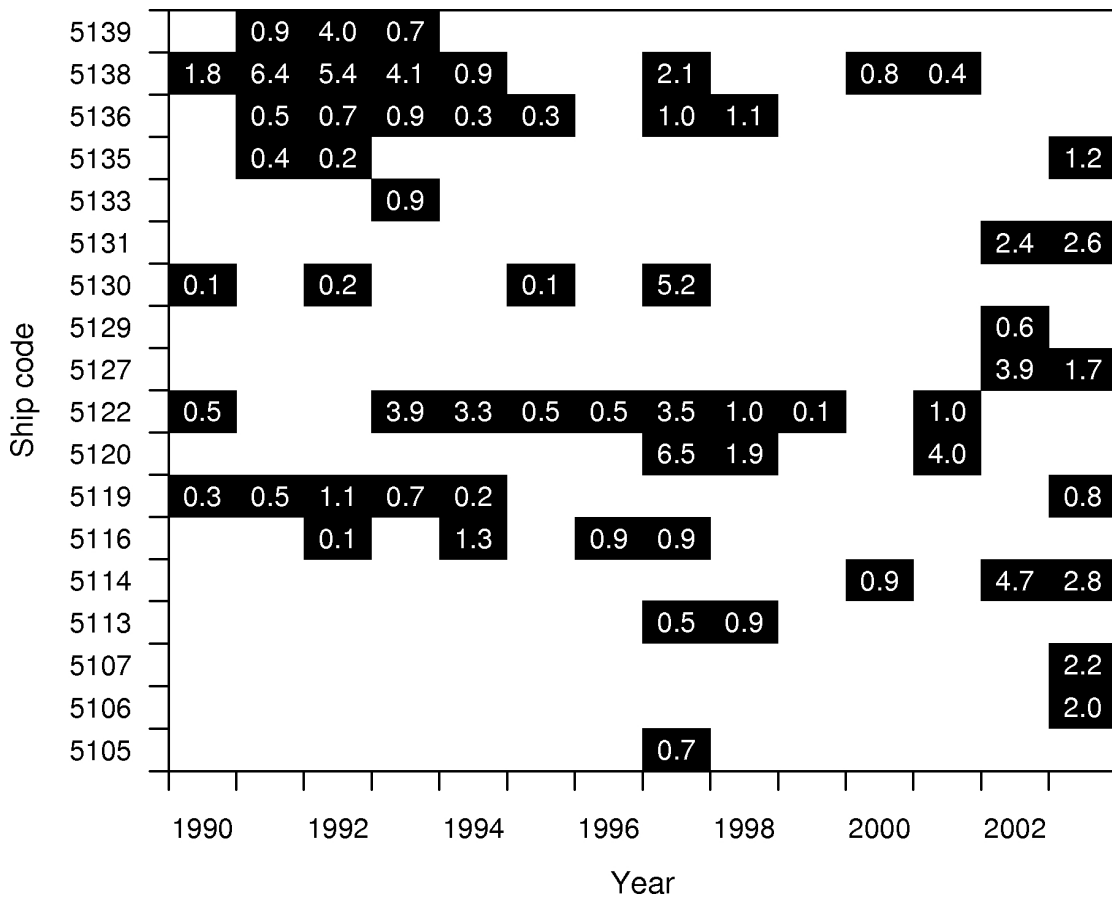


Figure 2.3. Distribution of survey effort among ships for data subset 5 (Table 2.1). Black bars indicate years in which individual ships were used for survey effort. Numbers within the bars indicate the percentage of total effort represented by that ship in that year.

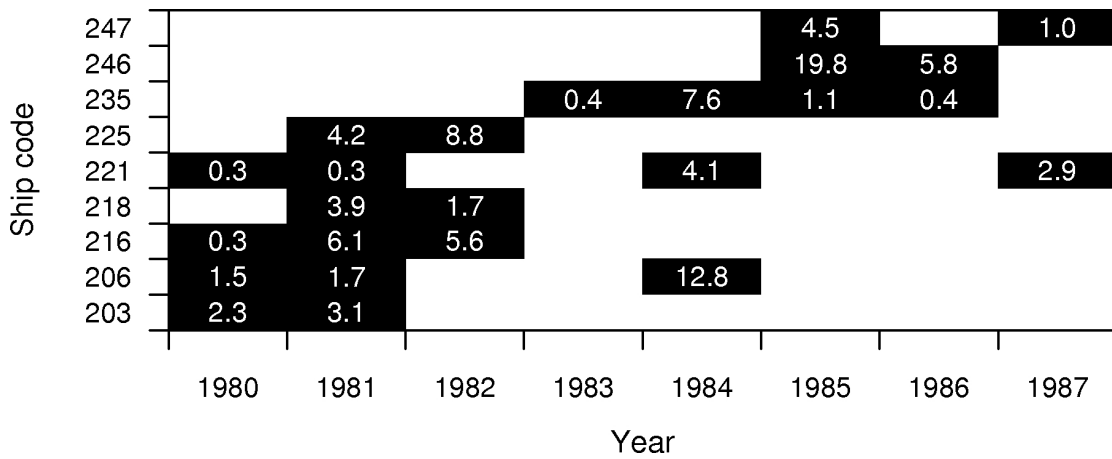


Figure 2.4. Distribution of survey effort among ships for data subset 7 (Table 2.1). Black bars indicate years in which individual ships were used for survey effort. Numbers within the bars indicate the percentage of total effort represented by that ship in that year.

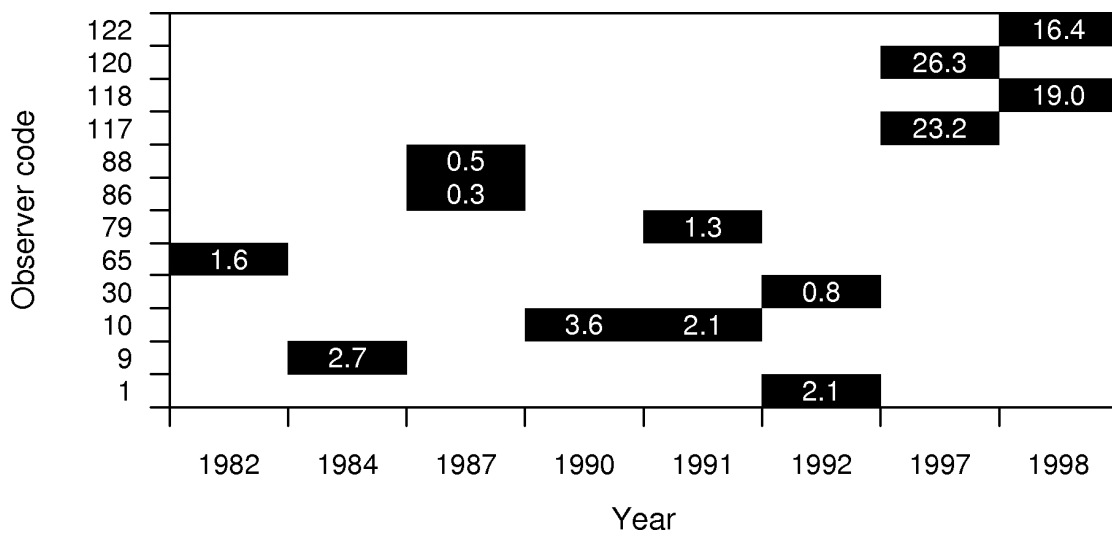


Figure 2.5. Distribution of survey effort among observers for data subset 1 (Table 2.1). Black bars indicate years in which individual observers had survey effort. Numbers within the bars indicate the percentage of total effort represented by that observer in that year.

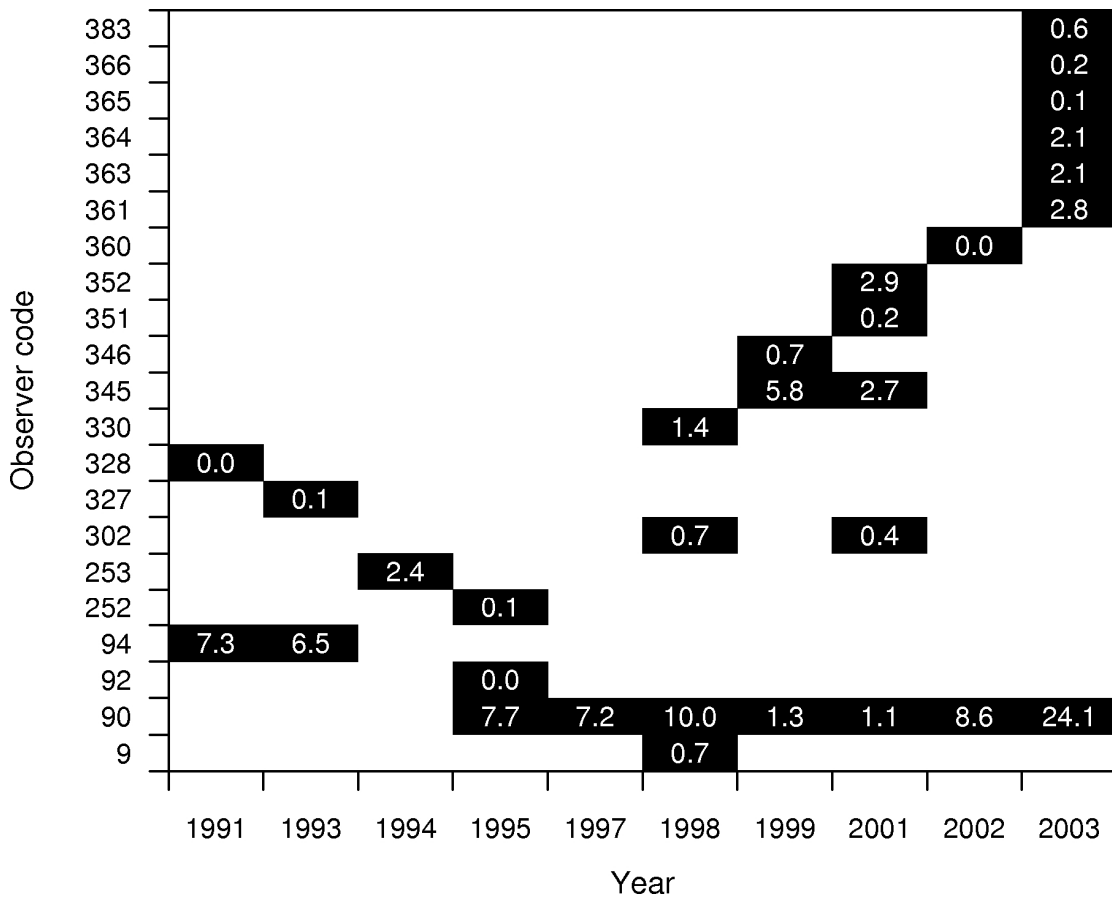


Figure 2.6. Distribution of survey effort among observers for data subset 2 (Table 2.1). Black bars indicate years in which individual observers had survey effort. Numbers within the bars indicate the percentage of total effort represented by that observer in that year.

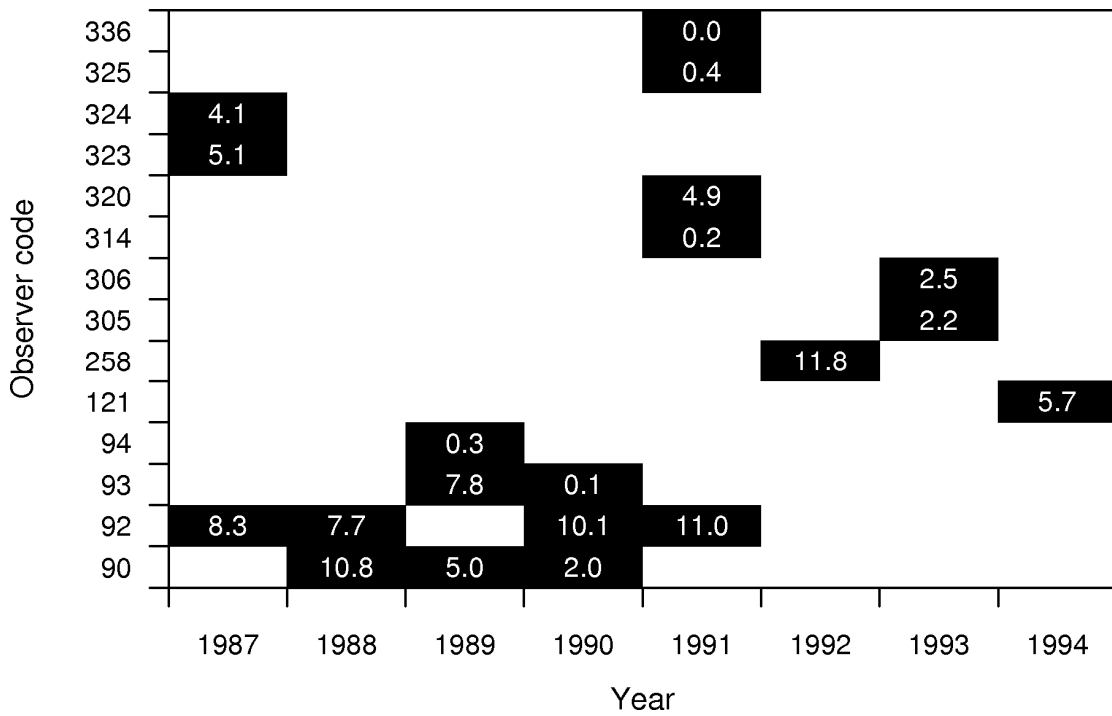


Figure 2.7. Distribution of survey effort among observers for data subset 3 (Table 2.1). Black bars indicate years in which individual observers had survey effort. Numbers within the bars indicate the percentage of total effort represented by that observer in that year.

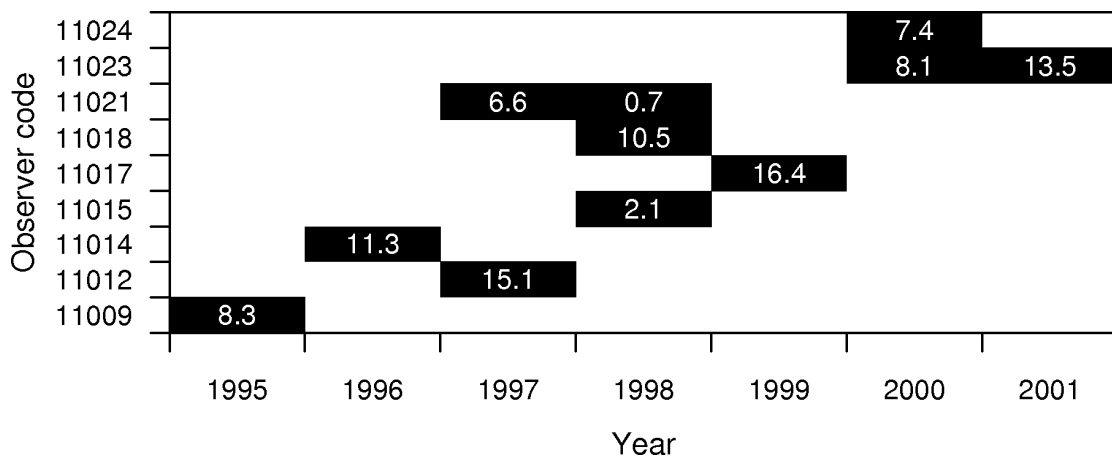


Figure 2.8. Distribution of survey effort among observers for data subset 4 (Table 2.1). Black bars indicate years in which individual observers had survey effort. Numbers within the bars indicate the percentage of total effort represented by that observer in that year.

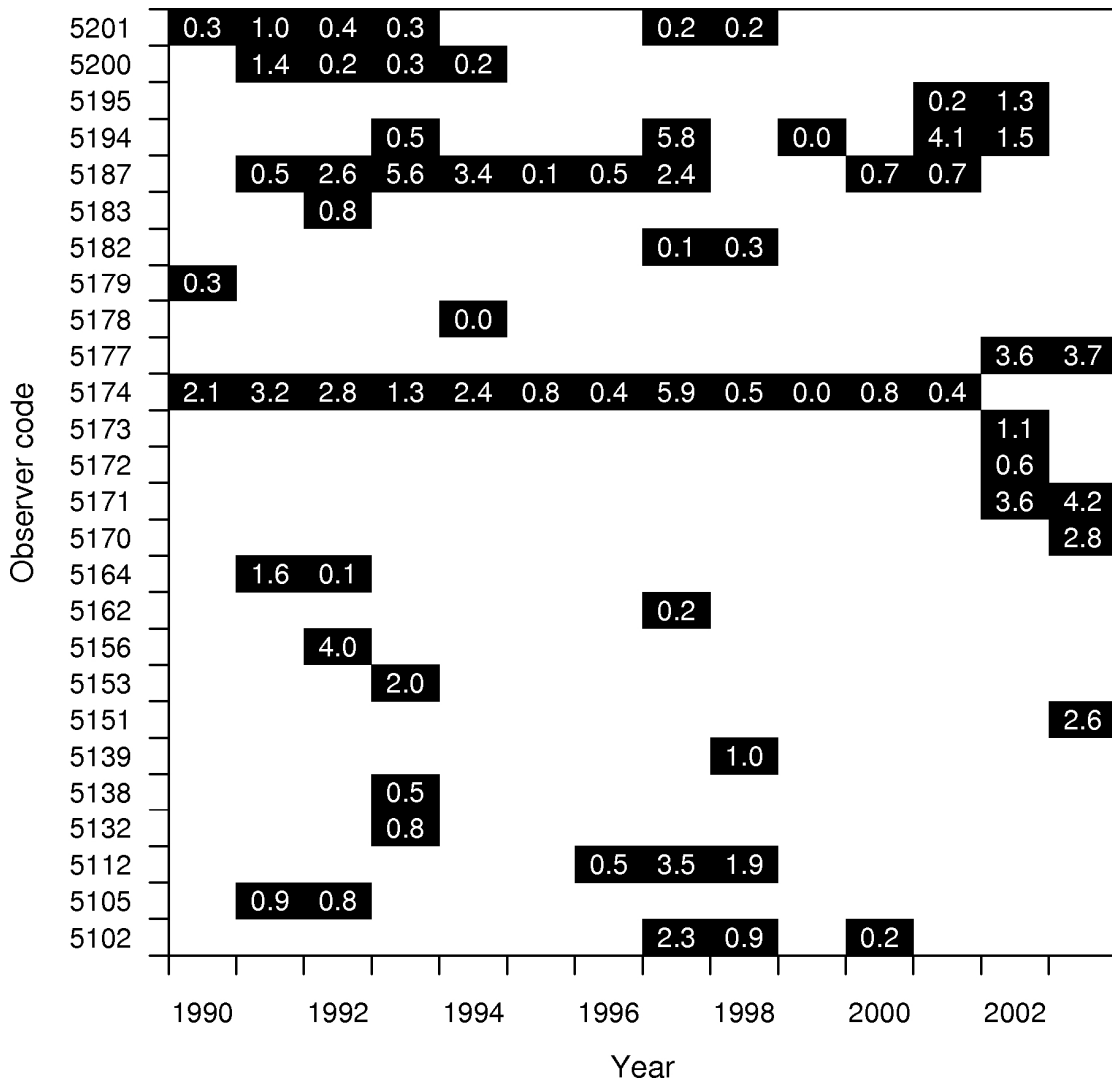


Figure 2.9. Distribution of survey effort among observers for data subset 5 (Table 2.1). Black bars indicate years in which individual observers had survey effort. Numbers within the bars indicate the percentage of total effort represented by that observer in that year.

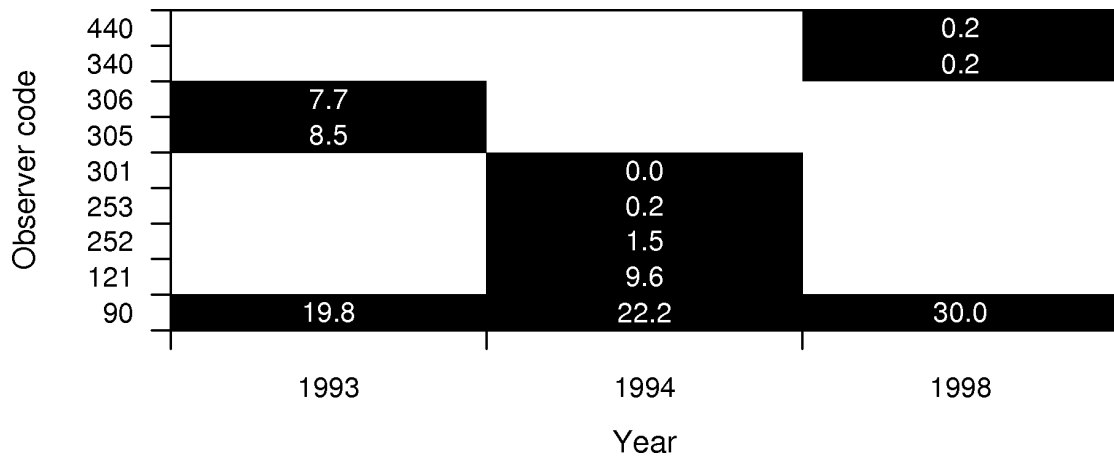


Figure 2.10. Distribution of survey effort among observers for data subset 6 (Table 2.1). Black bars indicate years in which individual observers had survey effort. Numbers within the bars indicate the percentage of total effort represented by that observer in that year.

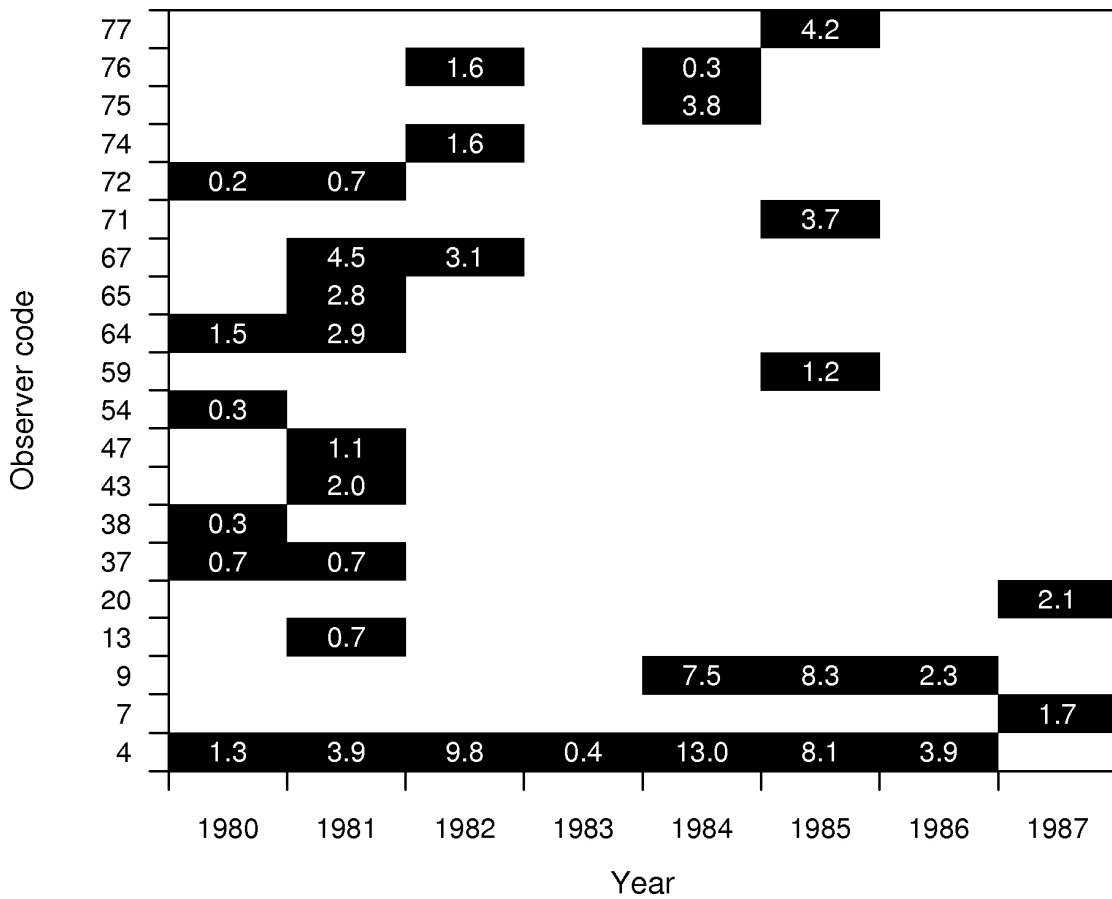


Figure 2.11. Distribution of survey effort among observers for data subset 7 (Table 2.1). Black bars indicate years in which individual observers had survey effort. Numbers within the bars indicate the percentage of total effort represented by that observer in that year.

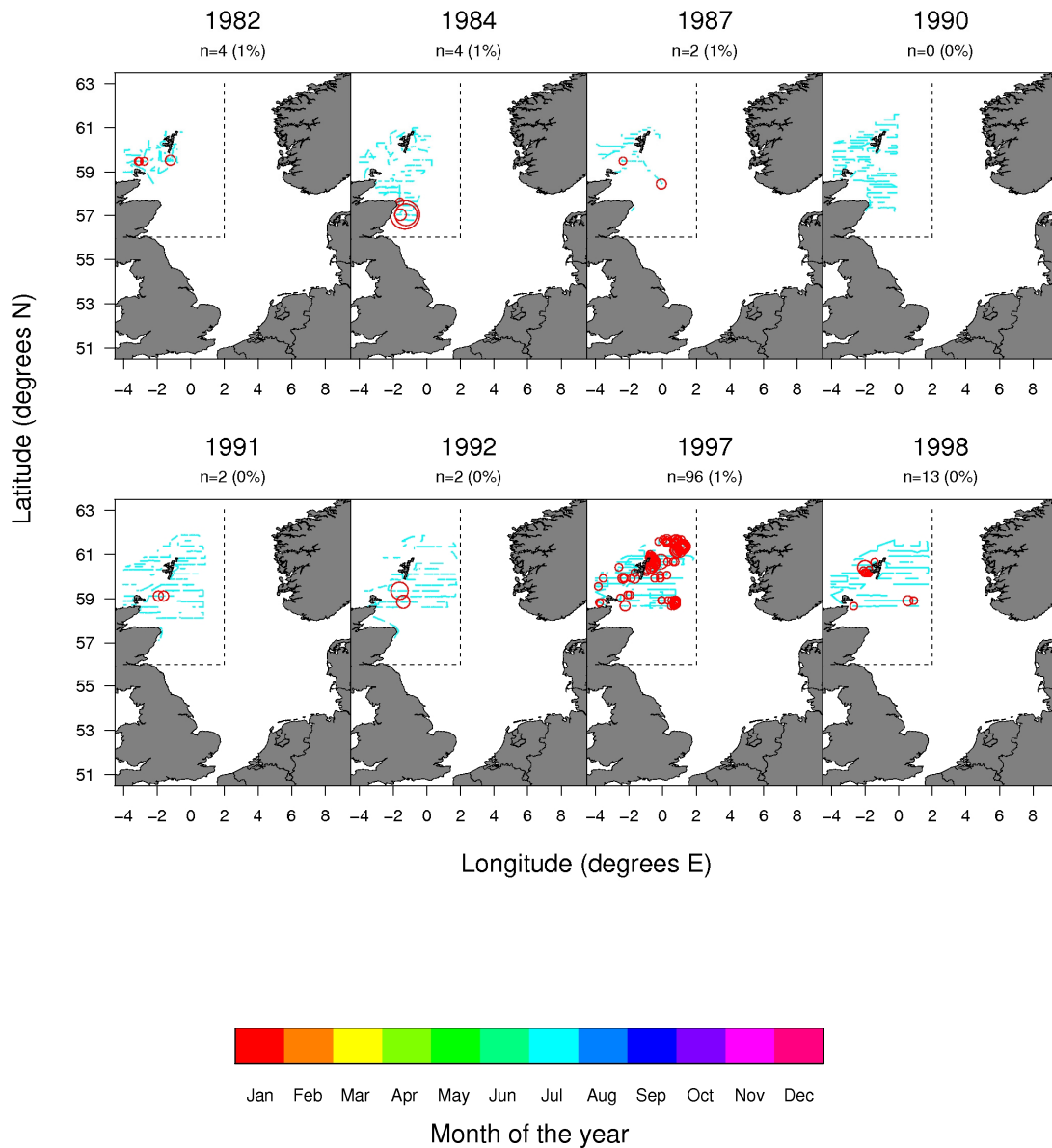


Figure 2.12. Geographic distribution of survey effort and harbour porpoise sightings by year for data subset 1 (Table 2.1). Coloured area indicates survey effort and red circles indicate recording periods with sightings. The size of a circle is proportional to the number of animals sighted during that recording period (scaled to the power of 0.4 for illustrative purposes). Number of recording periods with sightings (n) and the percentage of recording periods with sightings are indicated for each year.

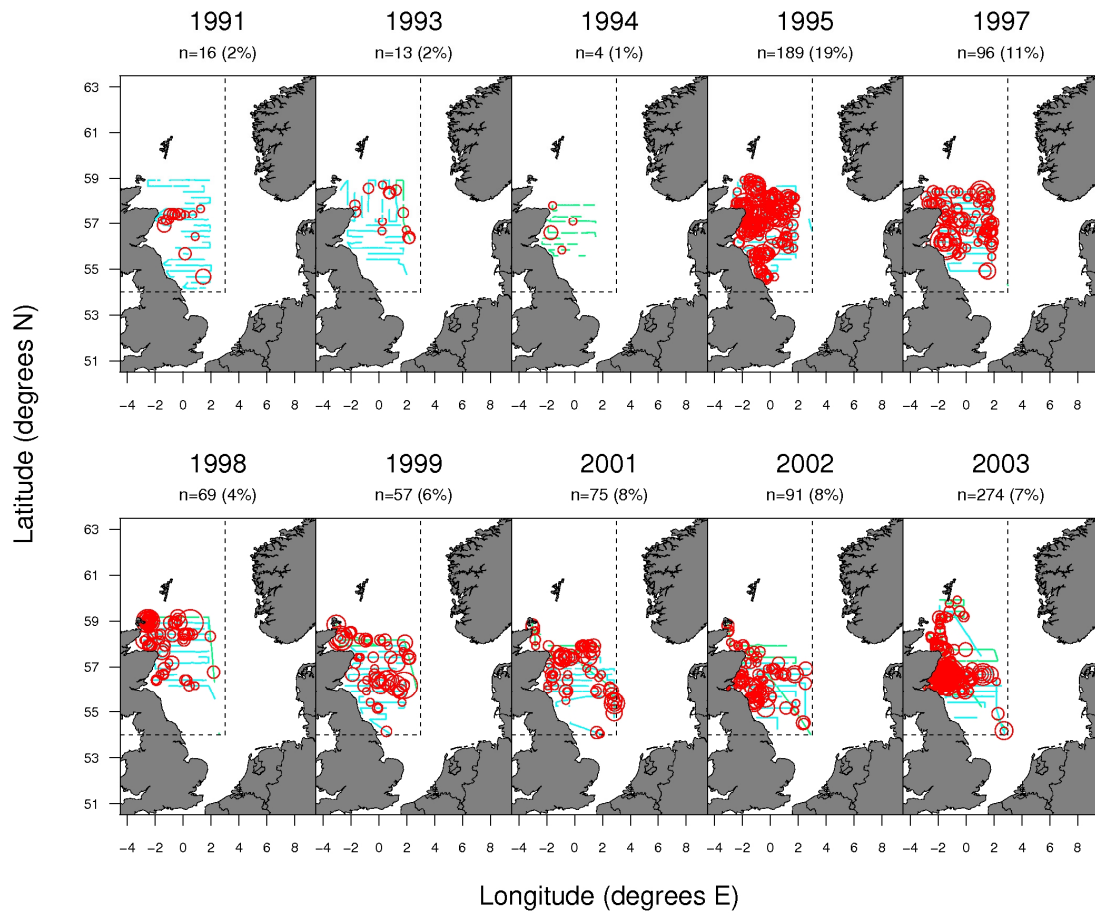


Figure 2.13. Geographic distribution of survey effort and harbour porpoise sightings by year for data subset 2 (Table 2.1). Coloured area indicates survey effort and red circles indicate recording periods with sightings. The size of a circle is proportional to the number of animals sighted during that recording period (scaled to the power of 0.4 for illustrative purposes). Number of recording periods with sightings (n) and the percentage of recording periods with sightings are indicated for each year. Survey effort colour legend is shown in Fig. 2.12.

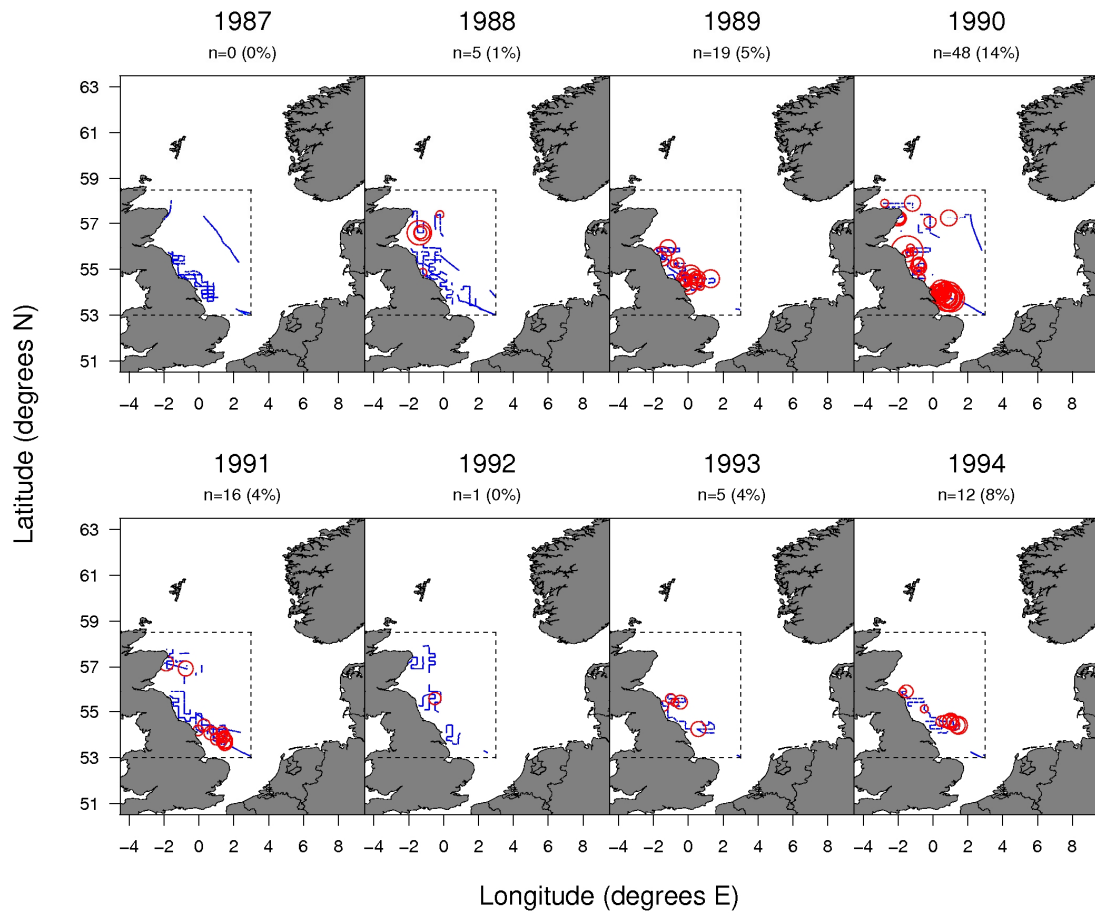


Figure 2.14. Geographic distribution of survey effort and harbour porpoise sightings by year for data subset 3 (Table 2.1). Coloured area indicates survey effort and red circles indicate recording periods with sightings. The size of a circle is proportional to the number of animals sighted during that recording period (scaled to the power of 0.4 for illustrative purposes). Number of recording periods with sightings (n) and the percentage of recording periods with sightings are indicated for each year. Survey effort colour legend is shown in Fig. 2.12.

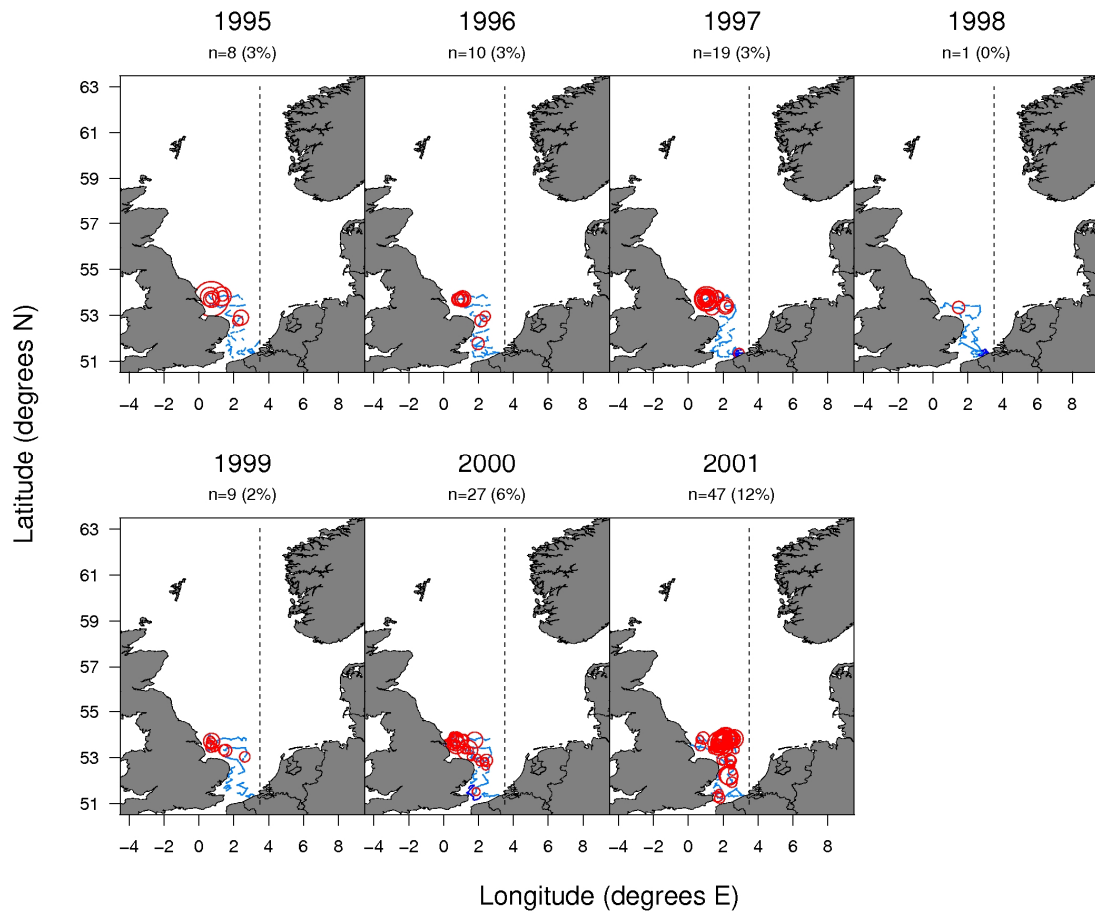


Figure 2.15. Geographic distribution of survey effort and harbour porpoise sightings by year for data subset 4 (Table 2.1). Coloured area indicates survey effort and red circles indicate recording periods with sightings. The size of a circle is proportional to the number of animals sighted during that recording period (scaled to the power of 0.4 for illustrative purposes). Number of recording periods with sightings (n) and the percentage of recording periods with sightings are indicated for each year. Survey effort colour legend is shown in Fig. 2.12.

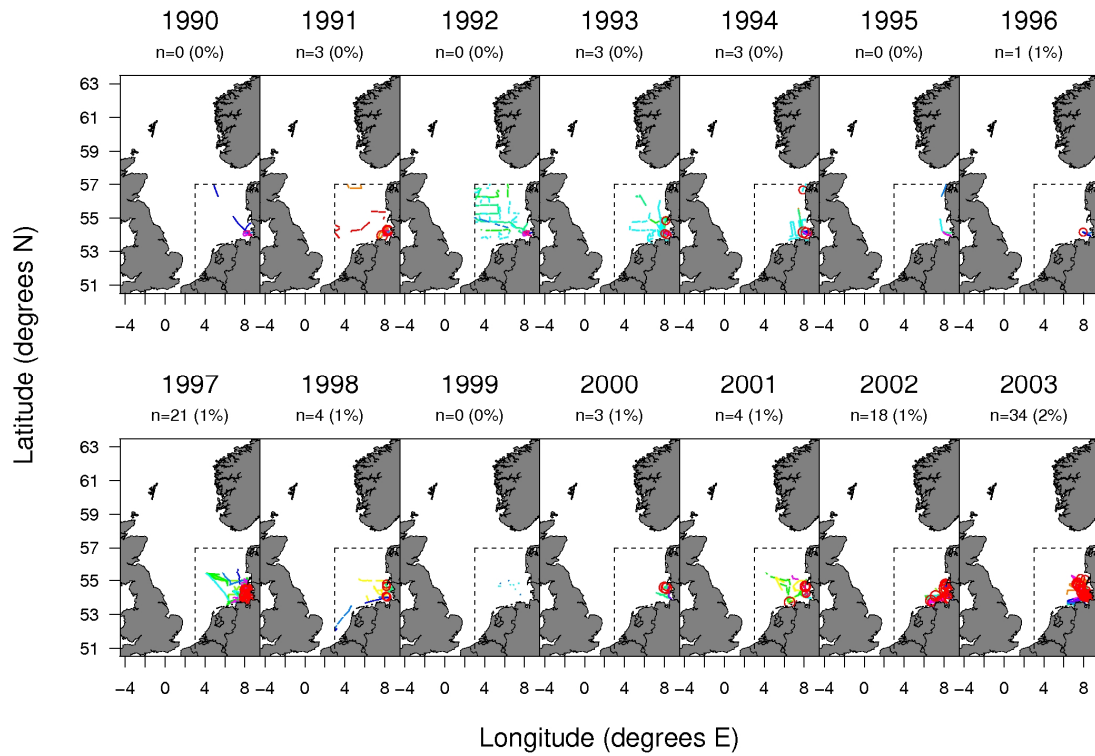


Figure 2.16. Geographic distribution of survey effort and harbour porpoise sightings by year for data subset 5 (Table 2.1). Coloured area indicates survey effort and red circles indicate recording periods with sightings. The size of a circle is proportional to the number of animals sighted during that recording period (scaled to the power of 0.4 for illustrative purposes). Number of recording periods with sightings (n) and the percentage of recording periods with sightings are indicated for each year. Survey effort colour legend is shown in Fig. 2.12.

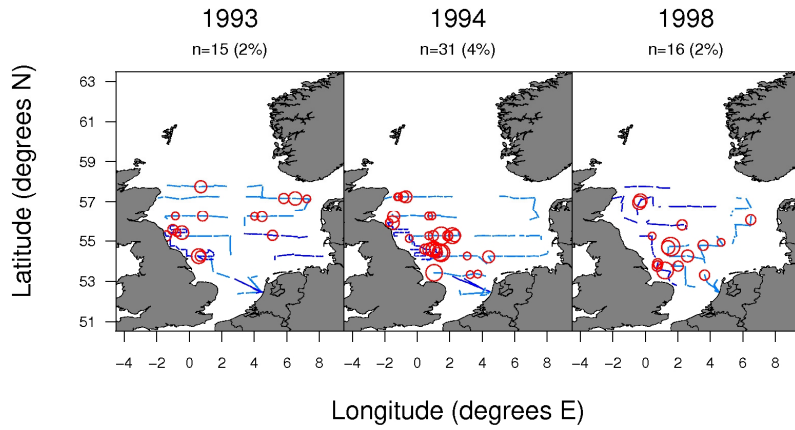


Figure 2.17. Geographic distribution of survey effort and harbour porpoise sightings by year for data subset 6 (Table 2.1). Coloured area indicates survey effort and red circles indicate recording periods with sightings. The size of a circle is proportional to the number of animals sighted during that recording period (scaled to the power of 0.4 for illustrative purposes). Number of recording periods with sightings (n) and the percentage of recording periods with sightings are indicated for each year. Survey effort colour legend is shown in Fig. 2.12.

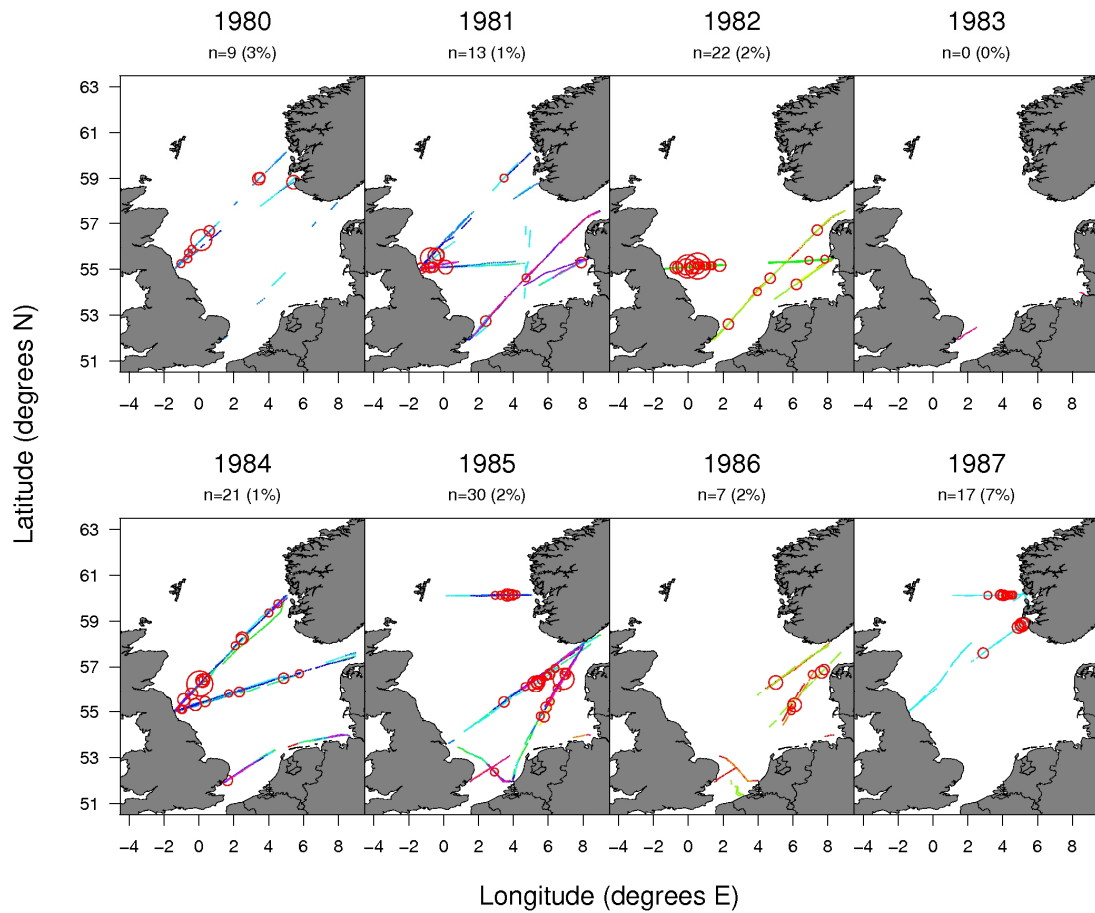


Figure 2.18. Geographic distribution of survey effort and harbour porpoise sightings by year for data subset 7 (Table 2.1). Coloured area indicates survey effort and red circles indicate recording periods with sightings. The size of a circle is proportional to the number of animals sighted during that recording period (scaled to the power of 0.4 for illustrative purposes). Number of recording periods with sightings (n) and the percentage of recording periods with sightings are indicated for each year. Survey effort colour legend is shown in Fig. 2.12.

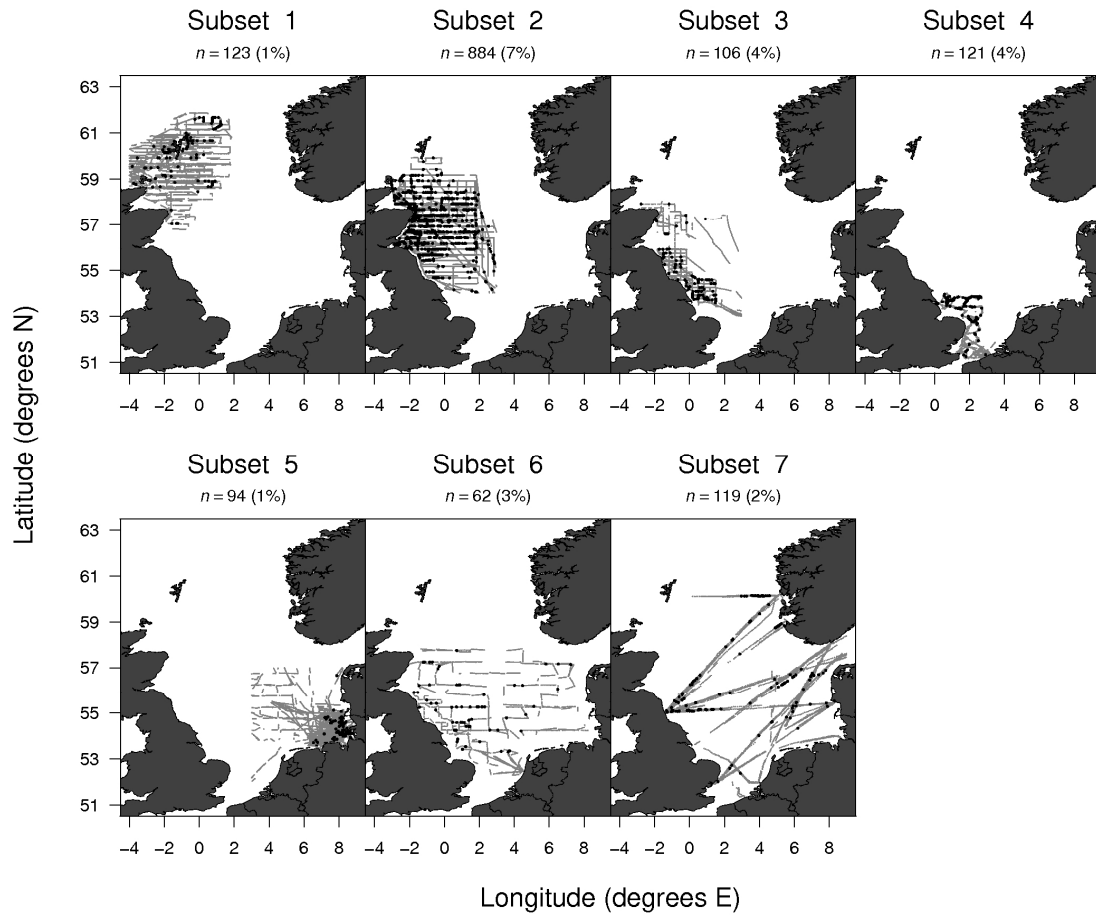


Figure 2.19. Geographic distribution of survey effort and harbour porpoise sightings for each data subset (Table 2.1). Light grey area indicates survey effort and black points indicate recording periods with sightings. Number of recording periods with sightings (n) and the percentage of recording periods with sightings are indicated for each subset.

Two important variables were not explicitly included in the statistical models: ship and observer. The physical characteristics of ships and the identity of observers can have strong effects on sighting rates. The height and view of the observation platform can affect sightability and the noise produced by a ship can affect the behaviour (and thus sightability) of animals. Individual observers can vary widely in their efficiency and experience at sighting animals. Ship and observer effects could be modelled statistically in several ways including fixed factors, random effects or generalized estimating equations. Unfortunately, it was not useful for me to model ship and observer effects because of the extremely heterogeneous and sometimes confounded nature of the data, particularly when ship, observer and year effects were completely confounded. I attempted to control for the effect of ship by analysing each data subset separately, but four of the subsets had data from multiple ships. Regardless, within all data subsets numerous observers were used for variable numbers of years and with variable degrees of overlap. The use of multiple simultaneous non-independent observers might have balanced out some potential observer effects. I explored potential biases in the estimated year effects that might have arisen from observer effects using mixed-effects models (described below).

The effect of binoculars was also difficult to model because in a given year binoculars were typically either always used or never used. Thus, any potential effect of binoculars on sightability was completely confounded with the effect of year on sighting rate. I only considered the use of binoculars in the statistical model for data subset 5; for the rest of the subsets I did not analyse data from years in which binoculars were used.

All other variables described in the previous section were considered for inclusion in the statistical models as well as interactions between longitude and latitude and between longitude, latitude and day of the year. The latter interaction was only considered when data covered a substantial part of the year. Distance travelled during the recording period was included as an offset so that the index of abundance was actually the number of harbour porpoise sighted per km. Sea state was treated as a continuous variable (Teilmann 2003). When individual levels of certain factor variables were represented by few data and/or were associated with no sightings, I excluded the data for these levels from the analysis (e.g., count type, transect width,

visibility). These data were excluded to minimize imbalances in data coverage and the number of zero data (and zero means). A year effect was always included in the model. I did not analyse data from years with no sightings as I was unable to obtain estimates of precision for the estimated sighting rates in those years. In exploratory modelling, the estimated mean sighting rates for those years were always very close to zero.

Models

Statistical modelling was done using generalized additive models in R for Windows (R Development Core Team 2007). A negative binomial likelihood (with log-link) was used because of the extremely high proportion of recording periods in which no harbour porpoise were sighted and the overdispersion of the data relative to the Poisson distribution (glm.nb function in MASS package; Venables and Ripley 2002). The negative binomial likelihood is commonly used for overdispersed count data and is a true likelihood (White and Bennetts 1996, James et al. 2006, Ver Hoef and Boveng 2007). The use of a zero-inflated negative binomial likelihood was also explored but the precision and significance of the zero-inflation parameter was generally low suggesting that a negative binomial likelihood was sufficient (zeroinfl function in pscl package; Jackman 2007, Zeileis et al. 2007). Another modelling option would have been a hurdle model combining a binomial likelihood for presence/absence and a zero-truncated likelihood for count when present (Martin et al. 2005). I chose the negative binomial likelihood for its simpler and more straightforward interpretation.

Non-linear relationships were incorporated in the statistical models using natural cubic splines defined by b-spline bases with fixed degrees of freedom (ns function in splines package). Degrees of freedom were limited to a maximum of 4 (i.e., 3 interior knots) per spline. Interior knots were placed at evenly spaced quantiles of the data (e.g., 25th, 50th, and 75th quantiles for 3 knots). Identical numbers of knots were used for splines for longitude and latitude. Tensor products were used to specify interactions between splines for longitude, latitude and day of the year. For example, the model term for an interaction between 3-degree-of-freedom splines for longitude and latitude would use an additional 9 degrees of freedom. To limit model complexity, I did not consider interactions between 3- and 4-degree-of-freedom

splines for longitude and latitude in terms where longitude and latitude interacted with day of the year. Cyclic splines provide more realistic representations of the effects of time of day and day of year whereby effects are constrained to be continuous throughout a day/year. However, data were only collected during daylight which did not span 24 hours. Similarly, survey effort spanned ≤ 2 months for 5 of the 7 data subsets (Table 2.1). Thus, cyclic splines were neither necessary nor appropriate to describe the majority of time-of-day and day-of-year effects within the observed ranges of values for these variables. A cyclic spline might have been more appropriate for the day-of-year effect in the models for subsets 5 and 7, but to be consistent with the models for the other data subsets I used non-cyclic splines.

Models were fitted with all combinations of variables and degrees of freedom for splines. I only considered models for which the fitting algorithm converged. I defined the best model for each data subset as that with the lowest Akaike Information Criterion (AIC). Effects of explanatory variables (mean and standard error) were estimated for the best models using the effect function of the effects package (Fox 2003, 2007). Effects were averaged over the other explanatory variables in the model. The effect function was modified slightly to allow for an offset in the model formula and to set the 'dispersion' to that returned by the summary.negbin function as is done with the predict function (dispersion=1). For year effects I also calculated model-averaged effects considering all models with substantial support (AIC within 2 of the AIC of the best model; Burnham and Anderson 2002). Model-averaged mean effects and standard errors were calculated using Eqs 4.1 and 4.9, respectively, of Burnham and Anderson (2002) which weight each model's contribution by its Akaike weight.

Two potential sources of bias in the estimated year effects are: 1) autocorrelation of sightings data in time and space and 2) confounding of observer and year effects. Un-modelled correlation in the number of sightings over time could arise if animals were clustered in time and space at scales longer than an individual recording period, and if the modelled day-of-the-year and spatial effects were insufficiently flexible to describe this clustering. Such un-modelled correlation would lead to overestimates of the precision of modelled effects. I examined the raw data and residuals of the best models for autocorrelation among sequential recording periods (i.e., time/space correlation) using the acf function in R and the Wald-Wolfowitz run test (Hardin and

Hilbe 2003). To explore potential biases arising from the confounding of observer and year effects I fitted mixed-effects versions of the best models using the `glmmPQL` function (MASS package; Venables and Ripley 2002). Observer was treated as a random intercept effect which somewhat constrained the potential effects of observers by assuming that they were normally distributed. I used the estimated scale parameter for the negative binomial likelihood from the corresponding fixed-effects models because `glmmPQL` does not estimate this parameter. While mixed-effects models cannot eliminate the problem of complete confounding between year and observer effects, I was interested whether these models would predict different year effects than the fixed-effects models did. I did not calculate the precision of the estimated year effects in the mixed-effects models, but simulation and analytical approaches could be used to do so (Gray and Burlew 2007). The precision of the estimated mean sighting rate for each year would almost certainly be lower in the mixed-effects models.

Results

Best models

The best model describing the number of harbour porpoise sighted per km varied among the seven data subsets (Table 2.2). The best models explained up to 65% of the deviance in the data. The raw data exhibited significant autocorrelation in the number of animals sighted among sequential recording periods at $\alpha=0.05$, but the residuals of all but one best model did not. The residuals of the model for subset 2 exhibited some autocorrelation, but it was much less than the raw data. The Wald-Wolfowitz run test was significant for the residuals of all models, but this result was at least partially because of the nature of the data rather than substantial autocorrelation in the residuals *per se*. The number of sightings was very low overall, thus the estimated mean sighting rates were also very low—generally much less than one animal per km. As a result, almost all of the negative residuals represented zero data, while almost all of the positive residuals represented data with ≥ 1 animal sighted (similar to a situation with binomial data). Thus, no matter how well a model explained the sightings data, the pattern of positive and negative residuals was similar to the raw data.

Table 2.2. Best models of number of harbour porpoise sighted per recording period selected using AIC for each data subset. All models were forced to include a year term and log(Distance) as an offset. The degrees of freedom for each term are in parentheses. NA indicates that the term was not considered for the model. Percent deviance explained was calculated as $[1-(\text{residual deviance}/\text{null deviance})]\times 100$.

Subset	<i>n</i>	Terms											% deviance explained
		Year	Sea state	Visibility	Number of observers	Bird count type	Bird transect width	Binoculars	Speed	Time of daylight	Day of year	Longitude / latitude	
1	20029	factor (6)	linear (1)	factor (3)	NA	factor (1)	NA	NA	none	spline (2)	spline (4)	spline (24)	47
2	11422	factor (8)	spline (3)	factor (3)	none	factor (2)	none	NA	spline (4)	spline (2)	spline (4)	spline (24)	35
3	2038	factor (5)	spline (4)	none	factor (1)	NA	none	NA	none	spline (3)	none	splines for longitude (3) and latitude (3), no interaction	46

Table 2.2 contd.

Subset	<i>n</i>	Terms											% deviance explained
		Year	Sea state	Visibility	Number of observers	Bird count type	Bird transect width	Binoculars	Speed	Time of daylight	Day of year	Longitude / latitude	
4	2876	factor (6)	spline (3)	none	none	factor (1)	NA	NA	spline (3)	none	spline (4)	spline (24)	65
5	9847	factor (7)	spline (2)	none	none	NA	NA	none	linear (1)	none	splines for day of year (4), longitude (2) and latitude (2), interactions between day of year and longitude (8) and day of year and latitude (8)		34

Table 2.2 contd.

Subset	<i>n</i>	Terms											% deviance explained
		Year	Sea state	Visibility	Number of observers	Bird count type	Bird transect width	Binoculars	Speed	Time of daylight	Day of year	Longitude / latitude	
6	1244	factor (1)	linear (1)	none	none	NA	none	NA	spline (2)	linear (1)	none	linear with interaction (3)	29
7	6434	factor (6)	spline (4)	none	NA	factor (3)	NA	NA	none	none	no day of year term, spline for longitude/latitude (24)	37	

Sighting conditions were found to be important explanatory variables for sighting rate. Sea state was included in the best model for all seven data subsets (Table 2.2). The sighting rate of harbour porpoise decreased sharply from sea states 0-2, and was generally very low at higher sea states (Fig. 2.20). The model for subset 5 suggested an increase in sighting rate, although highly uncertain, at the highest sea states. This was a result of several sightings at sea states up to 6 and a relatively inflexible spline (2 degrees of freedom), which resulted in spurious predictions at the edge of the data range where there were few data and no sightings (sea state >6). Visibility was present in the best model for two data subsets (Table 2.2). However, only the model for subset 2 exhibited the expected response of monotonically increasing sighting rate with increasing visibility (Fig. 2.21).

The majority of best models included some aspect of bird survey design as an explanatory variable (Table 2.2). Number of observers was included in the model for subset 3 with two observers having a higher mean sighting rate of harbour porpoise than one observer (Fig. 2.22). Bird count type was present in the models for subsets 1, 2, 4 and 7. Mean sighting rates were higher for count type 2 (on water transect, no snapshot for flying birds) than count type 1 (full transect method with snapshot for flying birds) in the models for subsets 1, 2 and 4, while the highest mean sighting rates in the model for subset 7 were for count types 3 (all observations, but no transect operated) and 4 (presence/absence data) (Fig. 2.23).

Speed, relative time of daylight and day of year were each present in the best model for 4 subsets (Table 2.2). Greater than 95% of estimated speeds were <35km/h (<19 knots) for subsets 1-6. The mean estimated speed for subset 7 was higher because these data were collected from ferries (95% <45 km/h). The estimated effect of speed was not consistent across subsets (Fig. 2.24). The models for subsets 2 and 4 predicted higher mean sighting rates at lower speeds, but this trend was highly uncertain especially at the lower and upper ends of the observed range of speeds. The models for subsets 5 and 6 suggested an increase in sighting rate with speed, but the confidence intervals were wide. The estimated effect of relative time of daylight was somewhat more consistent across data subsets, but not entirely (Fig. 2.25). The best model for subsets 1 and 2 exhibited a convex effect of relative time of daylight on sighting rate with the highest estimated sighting rate in the middle half of daylight.

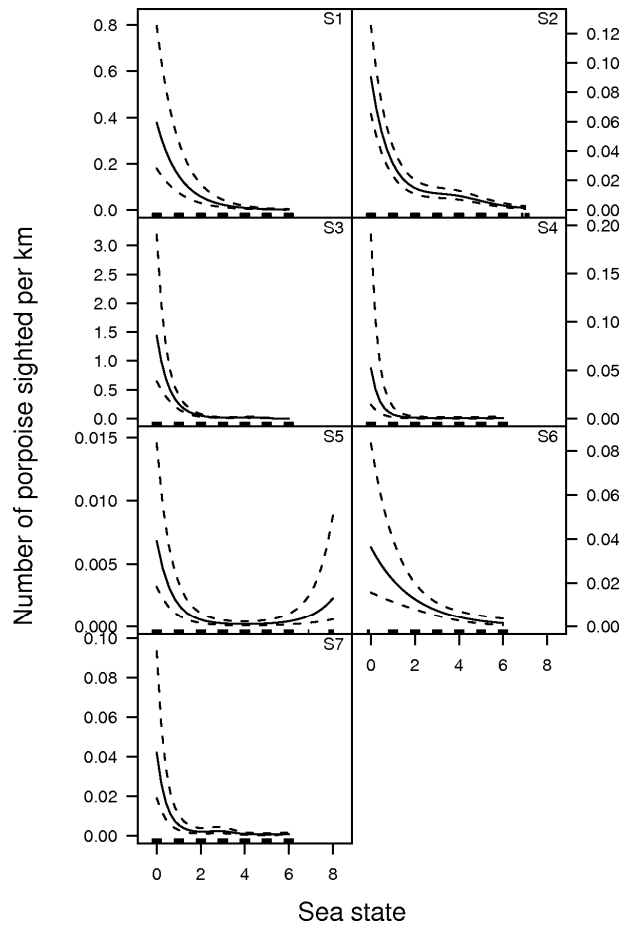


Figure 2.20. Effect of sea state on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Solid lines indicate the estimated mean sighting rate and dashed lines indicate the mean \pm 1 standard error (calculated on the scale of the link function and then converted to the response scale).

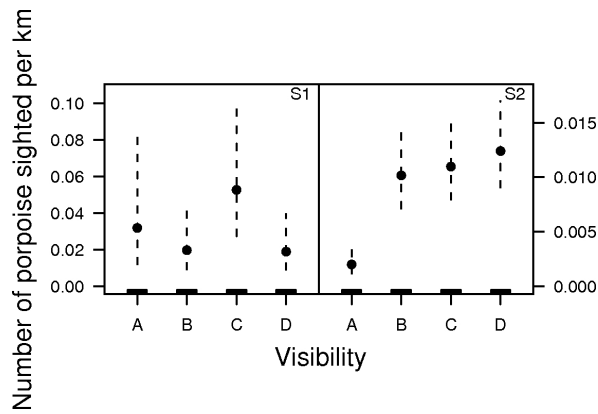


Figure 2.21. Effect of visibility on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Effects are only shown for models that had a visibility term (Table 2.2). Visibility code A represents the poorest visibility which increases to the best visibility at code D. Solid points indicate the estimated mean sighting rate and dashed lines indicate the mean \pm 1 standard error (calculated on the scale of the link function and then converted to the response scale).

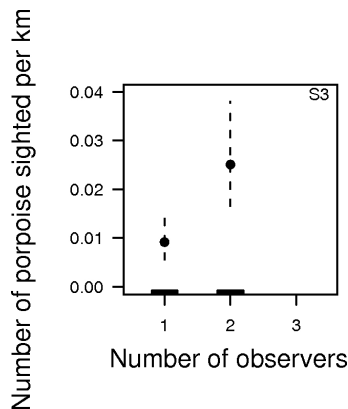


Figure 2.22. Effect of number of observers on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Effects are only shown for models that had a number of observers term (Table 2.2). Solid points indicate the estimated mean sighting rate and dashed lines indicate the mean \pm 1 standard error (calculated on the scale of the link function and then converted to the response scale).

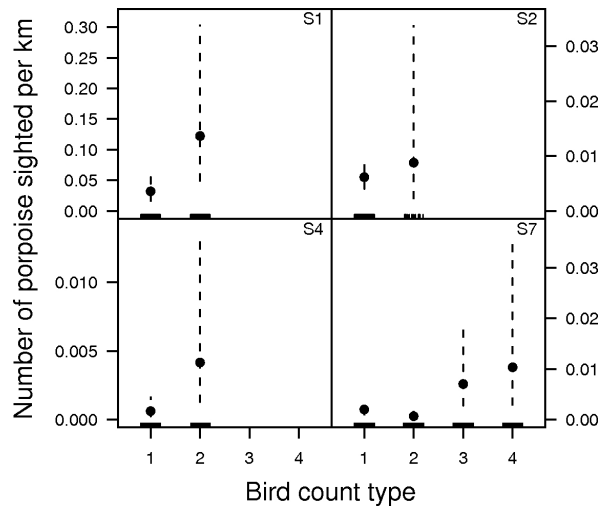


Figure 2.23. Effect of bird count type on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Effects are only shown for models that had a bird count type term (Table 2.2). Solid points indicate the estimated mean sighting rate and dashed lines indicate the mean \pm 1 standard error (calculated on the scale of the link function and then converted to the response scale).

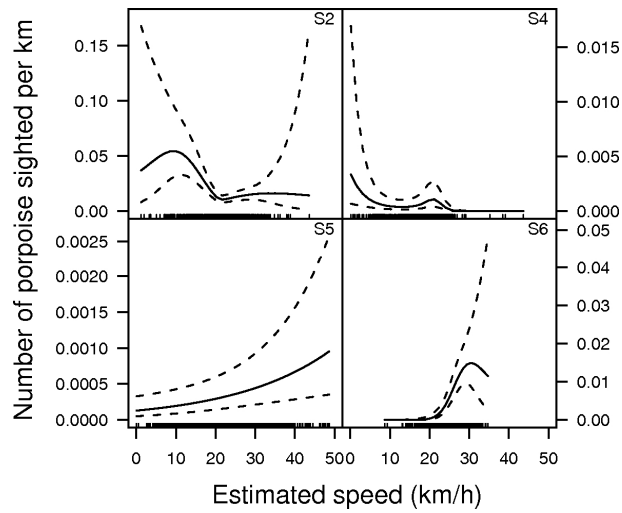


Figure 2.24. Effect of estimated speed on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Effects are only shown for models that had a speed term (Table 2.2). Solid lines indicate the estimated mean sighting rate and dashed lines indicate the mean \pm 1 standard error (calculated on the scale of the link function and then converted to the response scale).

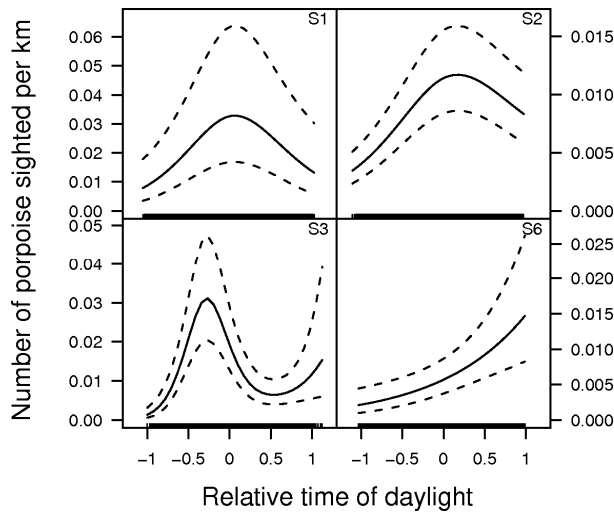


Figure 2.25. Effect of relative time of daylight on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Effects are only shown for models that had a relative time of daylight term (Table 2.2). A relative time of daylight of -1 corresponds to sunrise and 1 corresponds to sunset. Solid lines indicate the estimated mean sighting rate and dashed lines indicate the mean ± 1 standard error (calculated on the scale of the link function and then converted to the response scale).

The peak estimated sighting rate was slightly earlier in the day for subset 3 with very weak evidence of an increase in sighting rate near the end of daylight. Mean sighting rate simply increased with relative time of daylight in the model for subset 6. The estimated effect of day of the year varied across data subsets (Fig. 2.26). The model for subset 2 had the most well-defined peak in estimated mean sighting rate during the study period. For subset 5, the trend in estimated sighting rate by day of the year varied depending on location.

All of the best models included spatial effects on sighting rate (Table 2.2). The spatial component of the models for subsets 1, 2, 3 and 5 exhibited edge effects whereby the mean predicted sighting rate of harbour porpoise increased rapidly near a boundary of the study area (Fig. 2.27). Thus, predicted sighting rate was relatively even across the study areas for these subsets, although the model for subset 2 exhibited some areas of relatively higher sighting rates (e.g., off the east coast of Scotland between Peterhead and the Firth of Forth). The predicted effects of longitude and latitude on sighting rate varied by day of the year for subset 5, and edge effects were only evident at certain times of year. In the best model for subset 4, the estimated mean sighting rate was highest in the northernmost area surveyed off the east coast of England (near 54°N), and generally decreased with latitude resulting in the lowest estimated sighting rate in the southernmost North Sea. The surveys represented by subsets 6 and 7 covered much of the North Sea during the 1990s and 1980s, respectively. The models for both of these subsets estimated higher mean sighting rates in the western North Sea off the coast of Scotland and England (around 54-56°N) and in the eastern North Sea off southern Norway than in the central and southern North Sea. An interaction between day of the year and longitude/latitude was not included in the best model for subset 7 even though these surveys spanned much of the year.

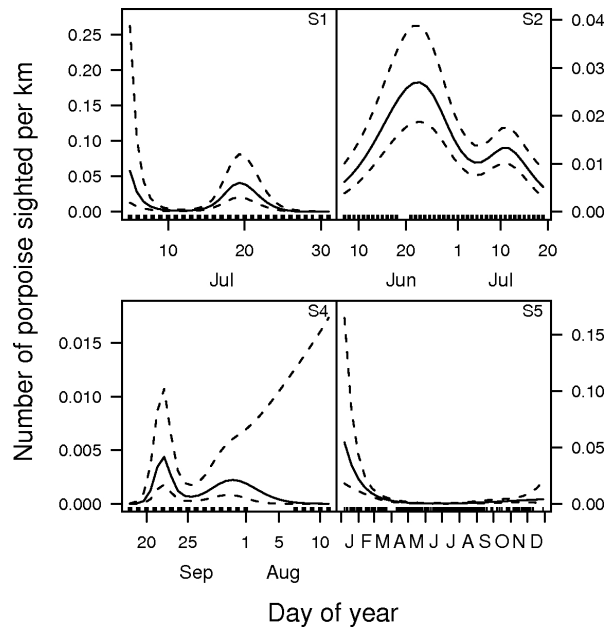


Figure 2.26. Effect of day of year on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Effects are only shown for models that had a day of year term (Table 2.2). Note that the effect of day of the year varied with longitude and latitude for subset 5 (the effect shown is for the mean longitude and latitude— 7.8°E , 54.2°N). Solid lines indicate the estimated mean sighting rate and dashed lines indicate the mean ± 1 standard error (calculated on the scale of the link function and then converted to the response scale).

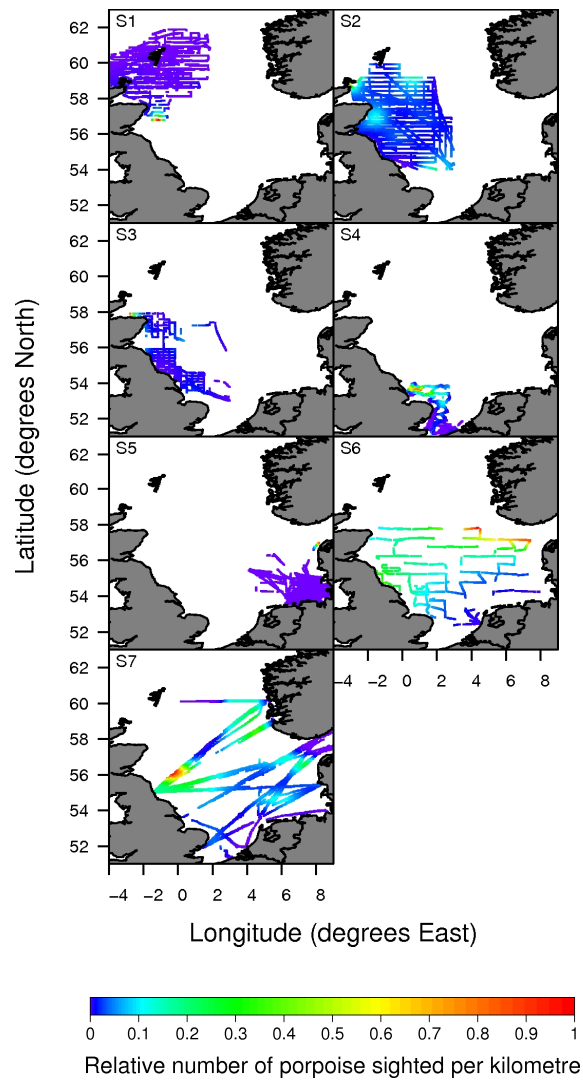


Figure 2.27. Relative effect of longitude and latitude on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top left corner of each panel; Table 2.1). Note that the effects of longitude and latitude varied with day of the year for subset 5 (the effect shown is for the mean day of the year—25 June).

Year effects

Best models

The estimated mean sighting rate of harbour porpoise was quite variable over time in the best models for all data subsets, even after controlling for the effects of other covariates (Fig. 2.28). There was no clear trend in sighting rate during summer from 1982-1998 in the northwest North Sea (subset 1). The model for summer in the western/northwestern North Sea (subset 2) had low estimated sighting rates in the early 1990s, but higher, decreasing sighting rates from the late 1990s through 2003. Another model for summer in the western North Sea during the late 1980s and early 1990s (subset 3) showed peak sighting rates from 1989 to 1991 preceded and followed by years with lower sighting rates. The model for summer in the southern/southwestern North Sea from 1995 onward exhibited the lowest sighting rates in 1997 and 1998, and the highest sighting rates at the end of the time-series in 2000 and 2001. The estimated mean sighting rate was generally higher from 2000 onward than during the 1990s in the southeast North Sea (subset 5). The mean estimated sighting rate was higher in 1998 than in 1993 in surveys spanning most of the North Sea (subset 6), and the mean estimated sighting rate from ferry surveys in the North Sea (subset 7) generally increased over time during the 1980s.

The precision of the estimated mean sighting rate of harbour porpoise for each year was generally low (Fig. 2.29). The highest precision observed with the best models was a CV of 0.37 (subset 2). However, more than half of the CVs were over 0.8. CVs tended to be higher for lower mean sighting rates, so the low overall sighting rate was likely one of the main reasons for the high CVs. It is important to note that I included year in all models in order to derive time-series of estimated mean sighting rates. It is possible that year would have been excluded from some of these models based on AIC.

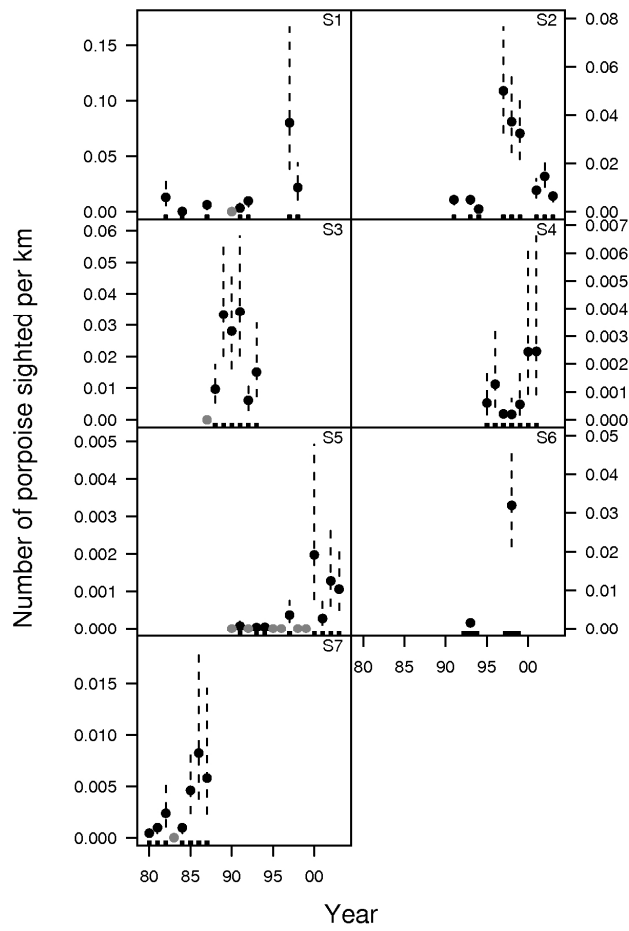


Figure 2.28. Effect of year on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Black points indicate the estimated mean sighting rate and dashed lines indicate the mean \pm 1 standard error (calculated on the scale of the link function and then converted to the response scale). Grey points indicate years with no sightings which were not modelled and in some cases were represented by few data.

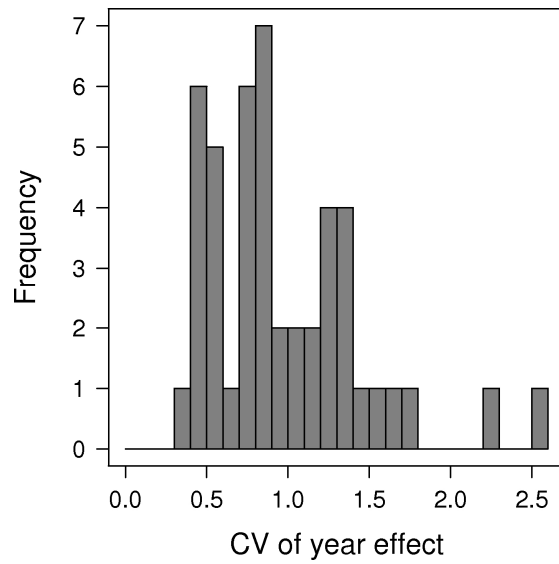


Figure 2.29. Histogram of CVs of year effects for all best models (Table 2.2). CVs were calculated assuming that the errors in estimated effects were normally distributed on the scale of the link function (log) so that $CV = \sqrt{e^{\sigma^2} - 1}$ where σ is the standard error on the scale of the link function.

Averaged models

For every data subset there was substantial support for several models based on AIC. The numbers of models with substantial support were 5, 12, 6, 3, 13, 18 and 4 for subsets 1-7, respectively. Model-averaged mean sighting rates and CVs by year were very similar to those from the best models (Fig. 2.30, 2.31). Model averaging did not change any of the aforementioned temporal patterns described from the best models. The lowest CV for estimated sighting rate in an individual year from the models considered for model averaging was 0.32.

Mixed-effects models

Estimated year effects from the best models and mixed-effects versions of these models were essentially identical for data subsets 1, 3, 4 and 6 (Fig. 2.32). The fitting algorithm estimated low variability in sighting rate among observers for these subsets and thus very small observer effects. In contrast, the mixed-effects model for subset 2 estimated lower year effects for the late 1990s through 2003 than the fixed-effects model, so the estimated mean sighting rates were closer to those in the early 1990s. This difference between the mixed-effects and fixed-effects models resulted from high estimated sighting rates for several observers who conducted much of the survey effort in the latter part of this time-series (observers 90, 345, 352 and 364; Fig. 2.6). The mixed-effects models for subsets 5 and 7 also estimated different year effects compared with the corresponding fixed-effects models because of variable observer sighting rates. The similarity in fits between the fixed-effects and mixed-effects models for 4 of the 7 data subsets illustrates the difficulty in estimating year and observer effects simultaneously when the two are confounded. Nevertheless, the mixed-effects models for subsets 2, 5 and 7 highlight the potential for bias in the estimated year effects because of observer effects. Furthermore, the precision of the estimated mean sighting rate for each year would be lower with these mixed-effects models.

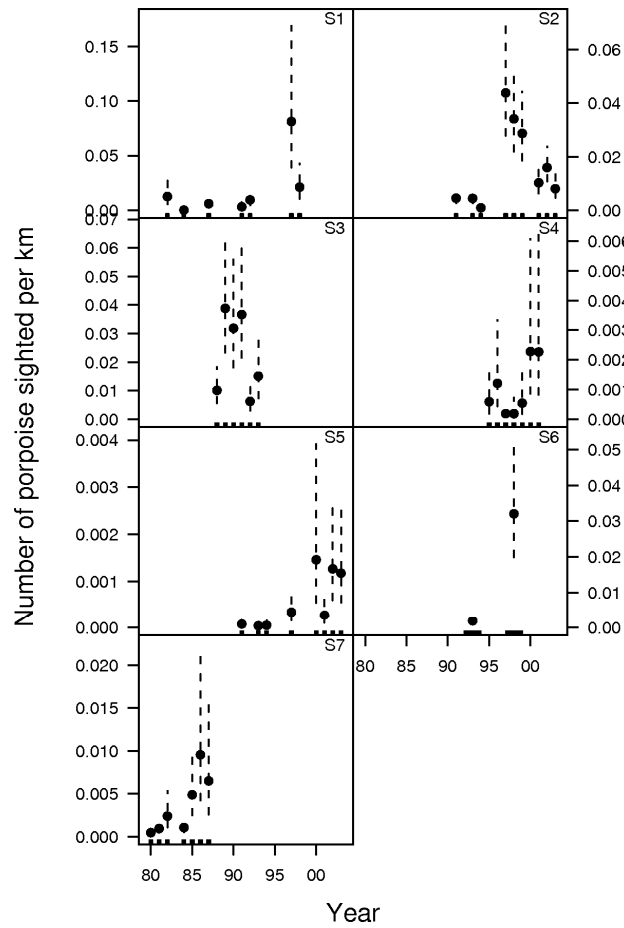


Figure 2.30. Model-averaged effect of year on the rate of sighting harbour porpoise for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Solid points indicate the estimated mean sighting rate and dashed lines indicate the mean \pm 1 standard error (calculated on the scale of the link function and then converted to the response scale). Note that years with no sightings are not shown.

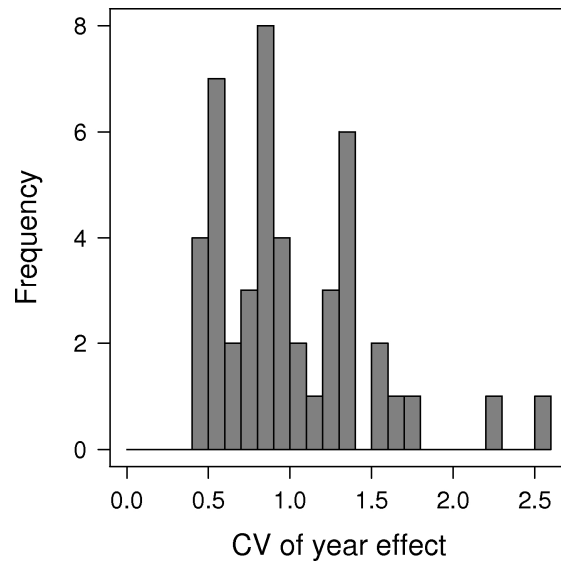


Figure 2.31. Histogram of CVs of model-averaged year effects. CVs were calculated assuming that the model-averaged errors in estimated effects were normally distributed on the scale of the link function (log) so that $CV = \sqrt{e^{\sigma^2} - 1}$ where σ is the model-averaged standard error on the scale of the link function.

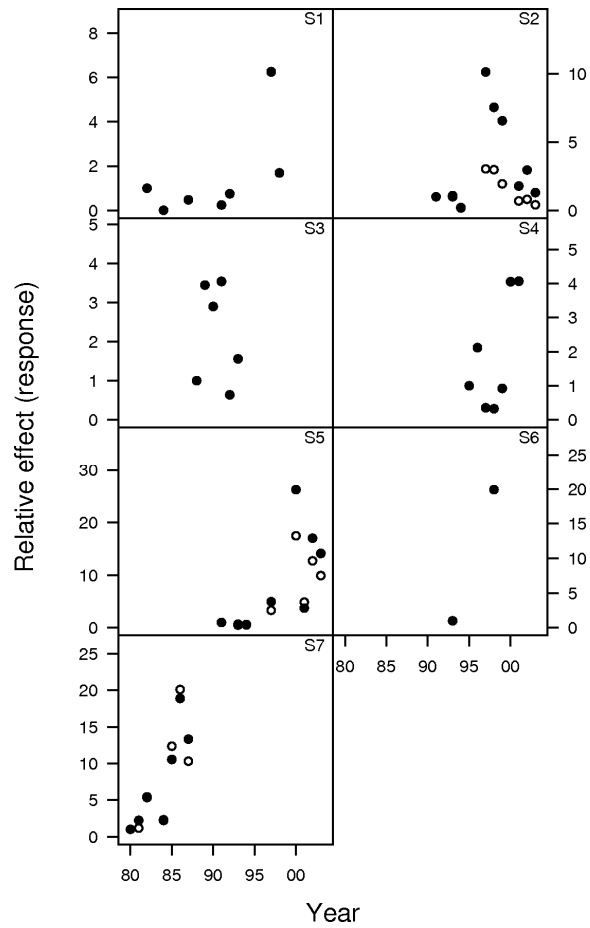


Figure 2.32. Relative effect of year (on the scale of the response) in the best fixed-effects model (filled points) and corresponding mixed-effects model (open points) for each data subset (subset is indicated in the top right corner of each panel; Table 2.1). Points indicate the estimated coefficient for each year relative to the first year, which equals 1. Open points that are not visible indicate identical effects. Note that years with no sightings are not shown.

Discussion

Many of the estimated patterns and trends in the sighting rate of harbour porpoise in the North Sea from the ESAS database were consistent with the findings of previous studies. For example, it is well known that the ability of visual observers to detect harbour porpoise is much better at low sea states (≤ 1) than high sea states (Teilmann 2003). In three of four models with a relative time of daylight term, sighting rate was highest in the middle half of daylight, which has been observed previously (Embling 2007). Spatial patterns in sighting rates were also broadly consistent with previous observations. I found higher estimated sighting rates off the coasts of Scotland and England and off the coasts of Denmark and Norway than in the central North Sea during summer. Predictions of the relative density of harbour porpoise in the North Sea based on two cetacean line transect surveys in July 1994 and 2005 were similar (SCANS-II 2008).

Some of the estimated patterns in the sighting rate of harbour porpoise were not expected. For example, in one model increasing visibility did not produce an increase in mean sighting rate. Furthermore, estimated trends in sighting rate with some variables, such as speed, were inconsistent across data subsets. The most likely reason for these unexpected results is that these explanatory variables were acting as proxies for other un-modelled variation in sighting rate. For example, ships might have encountered a particular visibility or been going at a particular speed when they entered an area of high harbour porpoise density that was not sufficiently captured by the year and spatial effects in the model. Thus, these estimated effects would not have been a result of visibility or speed *per se* but rather a result of variability in the spatiotemporal distribution of animals. Nevertheless, many of the estimated patterns in sighting rate were consistent with previous studies. Furthermore, a direct comparison of sighting rates of harbour porpoise by seabird observers and cetacean observers on the same ships found that the two were correlated (SCANS-II 2008). Thus, the ESAS database provides a useful resource for examining general patterns in harbour porpoise sighting rates in the North Sea.

Because I did not model groups of harbour porpoise separately, the estimated effects could be subject to group-size bias. Group-size bias is an issue with sightings data when larger groups of animals are more easily detectable than smaller groups

(Buckland et al. 2001). I did not correct for group-size bias because I did not have data on distances to the animals. Because I was only interested in relative abundance, the effect of group-size bias on the overall mean sighting rate was not an issue. However, group-size bias could still affect the relative relationships among levels of variables if mean group size varied with these variables. The mean size of harbour porpoise groups is small (1-2 animals; Hammond et al. 2002) and it seems unlikely that grouping behaviour (i.e., group structure) would change over time so group-size bias probably did not affect the observed trends in relative abundance across years. Nevertheless, the estimated effects of other variables on relative abundance might be subject to group-size bias if the size of porpoise groups varied with these variables (e.g., area or time of year).

In this study I was primarily interested in the usefulness of the ESAS database to provide time-series of relative abundance for harbour porpoise in the North Sea. Although estimated sighting rates were highly variable over time, there were at least a couple of temporal trends that were consistent with the results of previous studies. During the last 10-15 years, the number of harbour porpoise in the southern North Sea has apparently increased while the number in the northern North Sea has possibly decreased, at least during summer (Camphuysen 2004, SCANS-II 2008). The models for two areas in the southern North Sea (subset 4 - east coast of England and subset 5 - coasts of Germany, Denmark and Netherlands) suggested an increase in sighting rate from the late 1990s onward. One model for the western North Sea in summer (subset 2) suggested a decrease from the late 1990s onward—a period during which an individual observer accounted for much of the survey effort. However, estimated sighting rates in this subset were lowest during the early to mid-1990s. A potentially confounding factor affecting trends in sighting rates over time is observer experience. Sighting rates tended to be higher later in the time-series for most data subsets, and this might have been partially because observers became more efficient at sighting harbour porpoise over time, particularly in cases where individual observers were used for multiple years.

The precision of the estimated mean sighting rate for each year determines the amount of information that these indices of abundance provide about population dynamics over time. For example, in a surveillance monitoring framework that relies on the

detection of a statistically significant trend, less precise indices of abundance will decrease statistical power and increase the probability of concluding that there is no trend when in fact there is one (Gerrodette 1987). Similarly, less precise indices of abundance will provide less information to targeted and focused monitoring programmes that are components of conservation-oriented science and management (Nichols and Williams 2006). Seavy and Reynolds (2007) suggested that the precision of individual estimates should be the primary focus when evaluating population monitoring programmes. The precision of the annual mean sighting rates in my study ranged from CVs of 0.32-2.5. Overall, these are imprecise indices of abundance. However, CVs at the lower end of the range may provide decent statistical power to detect precipitous declines in population size if indices were available every year. For example, using the TRENDS software available at <http://swfsc.noaa.gov/prd.aspx> and assuming a 15-year study period and a CV proportional to $1/\sqrt{\text{abundance}}$, a CV of 0.32 would provide a statistical power of 0.7 to detect an exponential decline of 5% per year with a one-tailed hypothesis test at $\alpha=0.05$ (Gerrodette 1987, Taylor et al. 2007). However, this power drops to 0.47 if indices are only available every other year. It is more difficult to quantify how much information these indices would provide to more complex time-series and decision analysis as this would depend on the details of those analyses. An additional consideration in the fitting of any model to these time-series, including a simple trend model, is extra variability in the indices about the model predictions. Often the estimated CVs for indices of abundance are too small to describe all of the variability, so the amount of extra variability must be estimated (e.g., Wade 2002b). Additional variability would reduce the information provided by the indices.

I found that CVs tended to be higher for lower mean sighting rates, which suggested that the low overall sighting rate was one of the main reasons for the high CVs. It might be possible to increase the precision of the indices of abundance if more zero data are discarded. I did not consider levels of explanatory factor variables that were only associated with zero data, but one could eliminate further data associated with few sightings. For example, there were fewer sightings at high sea states, so the elimination of these data might increase the estimated mean sighting rates and the precision of those estimates. However, fewer data might also increase the CVs because of reduced degrees of freedom. The discarding of such data should not bias

results as long as there are no correlations between abundance and those explanatory variables (e.g., no correlation between abundance and sea state). It also might be possible to increase the precision of indices of abundance if multiple years are combined into a single estimate. One must then assume that abundance was the same during those years. Furthermore, the combination of multiple years would reduce the number of indices of abundance which would reduce the statistical power to model trend.

When standardising indices of abundance, additional explanatory variables will generally reduce bias, but will also decrease the precision of the indices (Thomas 1996, Maunder and Punt 2004). Thus, the CVs of the indices that I found are dependent on the method that I used to select model terms (AIC) and the maximum degrees of freedom that I allowed for model terms. An important explanatory variable that was not included in the models was observer identity. The illustrative mixed-effects models demonstrated the potential for bias in these time-series of relative abundance because of observer effects. If observer effects were large then not only could these estimates of sighting rates be biased, but their precision would be overestimated. Un-modelled sequential correlation in the number of animals sighted over time would also result in overestimation of the precision of the mean sighting rates. The residuals of my fitted models generally exhibited little autocorrelation, but the tests used were less than satisfactory for integer data with very small means. An alternative modelling approach that might have provided more appropriate CVs is non-parametric bootstrapping, but the proportion of zero data and the time required for model selection in a bootstrap framework were prohibitive.

There are further explanatory variables that I could have considered in the models of harbour porpoise sighting rate. For example, the number of birds in an observer's field of view could affect the observer's focus and ability to detect cetaceans. Larger numbers of birds could distract attention away from cetaceans resulting in lower sightability or larger numbers of birds could increase observer alertness resulting in better sightability (A. Webb, pers. comm.). Concurrent data on sighting rates of cetaceans by seabird observers and dedicated cetacean observers could potentially be used to evaluate effects of bird density on sightability (e.g., SCANS-II 2008). However, the number of birds in a given area or year might also be positively or

negatively correlated with the number of harbour porpoise in that area or year for any number of reasons; e.g., multi-species feeding aggregations, ecosystem linkages through prey dynamics, similar or dissimilar environmental preferences. If the numbers of birds and harbour porpoise were correlated then including the number of birds as an explanatory variable could negate the effect of interest (e.g., annual variation in abundance). The inclusion of data on other species when standardising indices of abundance may remove time trends which should be attributed to the year effect (Maunder and Punt 2004).

Environmental variables could also have been considered as explanatory variables in the models. Cetacean habitat modelling is an active area of research (Ferguson et al. 2006, Redfern et al. 2006). However, my objective was not to determine the ecological factors driving the distribution of harbour porpoise, but simply to account for differences in sighting rates in space within study areas when estimating temporal effects. Furthermore, correlations between environmental variables and harbour porpoise abundance could remove time trends in the same way that data on other species could. For example, if abundance is declining within a study area because of increased mortality or decreased reproduction driven by a change in an environmental variable then including that variable in a model of relative abundance may shed light on the mechanism of the decline, but would also eliminate the signal of a decline in a time-series of relative abundance standardised to a specific set of environmental conditions. Similarly, redistribution of animals into or out of a study area because of changes in environmental conditions can confound the standardisation of trends in abundance. Forney (1999) found that when temperature was included in a model of harbour porpoise sighting rates off California the year term dropped out of the model, suggesting that inter-annual variability was because of the redistribution of animals inside and outside of the study area driven by oceanographic conditions.

The time-series of relative abundance from this study (and future extensions of these time-series) could be used in several ways to assess the dynamics of harbour porpoise in the North Sea. The simplest use would be to monitor trends in relative abundance in specific areas, but as discussed above, the statistical power to detect changes is relatively low. Furthermore, it is likely that harbour porpoise move in and out of the geographic areas represented by most of the subsets of survey effort in my study

(Teilmann et al. 2004). Thus, any one of the time-series of relative abundance alone is not useful for monitoring the abundance of the population as a whole: redistribution of animals because of changes in density or environmental conditions would confound inferences about population trend (Blanchard et al. 2008). Analyses incorporating multiple time-series (e.g., Zuur et al. 2003) may provide more information about the population as a whole, but these may also be subject to low power.

A more appropriate use of the standardised time-series of relative abundance presented here would be to incorporate them in integrated population dynamics models that are also fitted to other available data such as absolute abundance and life history (Hoyle and Maunder 2004, Punt 2006, Tinker et al. 2006). Biological interpretation is more straightforward with explicit population models than with arbitrary trend models, and the addition of other data can improve the precision of estimates of abundance (Brooks et al. 2008). In Chapter 3 I develop such a model for harbour porpoise in the North Sea. Ideally, one would combine the standardisation of the indices of abundance and the population model in one statistical framework (Maunder 2001, Besbeas and Freeman 2006), however, this would be very computationally demanding with these data.

In summary, the ESAS database is a potentially useful source of information on general patterns and trends in harbour porpoise sighting rates in the North Sea. However, the standardised indices of abundance from these data had relatively low precision, thus they have limited value for a population monitoring framework that relies on statistical detection of trend. Nevertheless, these time-series of relative abundance might enhance integrated analyses of the dynamics of harbour porpoise populations in this area.

Chapter 3: Assessment of the population dynamics and conservation status of harbour porpoise in the North Sea using an integrated model to synthesize information on life history, abundance and bycatch

Introduction

An understanding of the dynamics of harbour porpoise populations is a prerequisite for assessing the impact of bycatch on their conservation status. Three quantities of particular interest are: 1) the bycatch removed from the population, 2) the size of the population, and 3) the rate at which the population can grow in the absence of bycatch (Stenson 2003). Estimates of these three quantities can simply be compared or they can be used in combination with a population model to assess the effect of bycatch on a population's conservation status in the past, present and future (Lewison and Crowder 2003, Kaplan 2005). While knowledge of these quantities is essential for management and conservation, estimates of these quantities are often lacking or highly uncertain.

Several studies have used estimates of the bycatch, size and growth rate of populations of harbour porpoise and other small cetaceans to compare bycatch mortality with production (Woodley and Read 1991, Woodley 1993, Caswell et al. 1998, Dans et al. 2003) and to develop models to assess the impact of bycatch on conservation status (Reijnders 1992, Mangel 1993, Barlow and Hanan 1995, Slooten et al. 2000). In general, bycatch, population size and population growth rate have been estimated independently. For example, estimates of population growth rate have often been derived from estimates of survival and reproductive rates based on life history data (e.g., Woodley and Read 1991). Estimates of bycatch have usually been treated as input to population models. In almost all cases, the estimation of bycatch, population size and population growth rate was subject to large uncertainties. Most previous studies have accounted for this uncertainty using Monte Carlo techniques and scenario analysis (Woodley and Read 1991, Caswell et al. 1998, Slooten et al. 2000).

An elegant approach to assessing the dynamics of a population is to fit a model to all relevant data simultaneously—an integrated population dynamics model (Myers et al. 1997, Goodman 2004, Besbeas and Freeman 2006, Polacheck et al. 2006, Punt 2006,

Tinker et al. 2006, Schaub et al. 2007). A population model ensures mathematical consistency among inferences about different aspects of population dynamics, and a model can be fitted to a diverse range of data on population size and life history. Embedding a population model in statistical inference allows appropriate representation of uncertainty in estimates of population dynamics (Hilborn and Mangel 1997, Buckland et al. 2007). Bayesian statistics are particularly useful for characterising uncertainty in population dynamics models (Walters and Ludwig 1994, Wade 2000, Harwood and Stokes 2003, Ellison 2004) and have been used frequently in the assessment of fish and marine mammal populations (Punt and Hilborn 1997, McAllister and Kirkwood 1998, Punt and Butterworth 1999, 2002, Wade 2002b, Witting and Born 2005, Brandon and Wade 2006, Skaug et al. 2008). A statistically fitted population dynamics model allows for seamless incorporation of estimation uncertainty into prediction for risk assessment, population viability analysis and management strategy evaluation (Harwood 2000, Maunder et al. 2000, Wade 2002a, Maunder 2004, Kaplan 2005). Bayesian integrated population dynamics models have been used previously to examine the impact of intentional and unintentional takes of small cetaceans (Alvarez-Flores and Heide-Jørgensen 2004, Hoyle and Maunder 2004). Pout et al. (2001) reported on a preliminary attempt to use a population model to examine the effect of bycatch on harbour porpoise in the North Sea.

While many data are available on the bycatch, abundance and life history of harbour porpoise in the North Sea, these datasets have mainly been analysed separately in the past. Estimates of bycatch were as high as thousands of porpoise per year during the 1990s (Vinther and Larsen 2004) and are the cause of conservation concern. A recent study of stranded and bycaught harbour porpoise from the Scottish coast of the North Sea found a relatively low pregnancy rate in a sample from 1992 onward (Learmonth 2006), which combined with the relatively short lifespan of harbour porpoise (Lockyer 1995b, Read and Hohn 1995) suggests a limited potential for population increase. However, best estimates of harbour porpoise abundance in the North Sea in July 1994 and 2005 were both around 200,000 animals with no statistically significant difference (Hammond et al. 2002, SCANS-II 2008), although the spatial distribution of harbour porpoise within the North Sea was different between the two surveys (SCANS-II 2008). To reconcile these various pieces of information and evaluate their consistency, some type of population model must be used.

The overall objective of this chapter was to develop an integrated population dynamics model for harbour porpoise in the North Sea from 1987-2005 and to use the model to assess the population dynamics and conservation status of the species in this area. I fitted the model to concurrent data on bycatch rate, abundance and life history to derive estimates of bycatch, population growth rate (with and without bycatch) and carrying capacity with appropriate estimates of uncertainty. The population model allowed me to evaluate the consistency of the different datasets and to examine the plausibility of different hypotheses regarding the dynamics of harbour porpoise populations in the North Sea.

Methods

Population model

The population model was an age-structured simulation of the female component of one or more subpopulations occupying non-overlapping geographic ranges with a time step of one calendar year. All births were assumed to occur simultaneously at the middle of each year (end of June).

First, simultaneous natural and bycatch mortalities were applied prior to births:

$$[3.1] \quad N_{a+1,i,t+0.5} = N_{a,i,t} e^{-\left(\frac{M_a + F_{a,i,t}}{2}\right)}$$

where $N_{a,i,t}$ is the number of animals of age a (years) in subpopulation i at the beginning of year t , M_a is the instantaneous natural mortality rate from age a to $a+1$ and $F_{a,i,t}$ is the instantaneous mortality rate as a result of bycatch from age a to $a+1$ in subpopulation i during year t . Eq. 3.1 assumes constant instantaneous mortality rates throughout the year.

Instantaneous natural mortality rates were calculated from estimated age-specific survival rates (s_a):

$$[3.2] \quad M_a = -\log(s_a)$$

Annual survival rates were estimated for four age groups: age 0; age 1; $2 \leq \text{age} < a^{\text{m50}}$; $a^{\text{m50}} \leq \text{age} \leq \omega$, where a^{m50} is the age at which 50% of females are sexually mature (estimated) and ω is the maximum age (fixed). I assumed knife-edge survival

senescence where all animals that survived to age $\omega+1$ died (naturally) at that age. An alternative approach to modelling age-specific survival rates is to use some continuous function of age. In a preliminary analysis I attempted to use Siler's competing-risk model to describe age-specific survival (Siler 1979, Barlow and Boveng 1991, Stolen and Barlow 2003), but I found that there was no strong signal of senescence in the mortality age structure data, and estimates of the immature and mature risk components were highly correlated. Thus, I decided to use age-specific survival rates.

Instantaneous bycatch mortality rates were calculated from input data on total fishing effort and estimated catchability and vulnerability parameters:

$$[3.3] \quad F_{a,i,t} = \eta_a \sum_{h=1}^H q_h E_{h,i,t}$$

where η_a is the vulnerability of an animal of age a to bycatch, q_h is a parameter specifying bycatch per unit effort in fishery h , $E_{h,i,t}$ is the total effort in fishery h in the range of subpopulation i during year t (input) and H is the total number of fisheries. Age-specific vulnerabilities were estimated for the same four age groups used in the estimation of natural survival. Age-specific vulnerability was fixed at 1 for age 1 and the vulnerabilities of the other three age groups (relative to age 1) were estimated. As with natural survival, I attempted to describe vulnerability as a continuous function of age including a double-logistic model (Quinn and Deriso 1999) and several unimodal probability distributions including lognormal, gamma and negative binomial (Millar and Fryer 1999). However, when these functions were fitted to the mortality age structure data, the best fits resulted in vulnerability simply decreasing with age while the raw data suggested peak vulnerability for 1-year-old animals. A more flexible unimodal function might have captured this peak, but I decided to use age-specific vulnerabilities instead.

Births were assumed to occur at the middle of each year (Van Utrecht 1978, Sørensen and Kinze 1994, Lockyer 1995b) so that:

$$[3.4] \quad N_{0,i,t+0.5} = b_{i,t} \sum_{a=1}^{\omega} N_{a,i,t+0.5} m_{a-1}$$

where $b_{i,t}$ is birth rate in subpopulation i during year t (number of female calves born per sexually mature female per year) and m_a is the proportion of females that are sexually mature at age a . The sexual maturity ogive was:

$$[3.5] \quad m_a = \left(1 + e^{\frac{a-a^{m50}}{\sigma^m}} \right)^{-1}$$

where σ^m is an estimated parameter specifying the width of the ogive. Eq. 3.4 assumes that birth rate does not vary with age and that females must be sexually mature for at least one year before giving birth.

Birth rate was assumed to be either density-independent or density-dependent. When birth rate was assumed to be density-independent, the birth rate did not vary over time. When birth rate was assumed to be density-dependent, the birth rate was calculated as:

$$[3.6] \quad b_{i,t} = \max \left[b^K + (b^{\max} - b^K) \left(1 - \left[\frac{\sum_{a=1}^{\omega} N_{a,i,t}}{N_i^{1+,K}} \right]^z \right), 0 \right]$$

where b^K is birth rate at carrying capacity, b^{\max} is maximum birth rate (estimated), $N_i^{1+,K}$ is the number of female non-calves at the beginning of the year at carrying capacity in subpopulation i (estimated), and z is a density-dependence shape parameter. Eq. 3.6 assumes that birth rate is a function of the number of non-calves alive at the beginning of the year. Birth rate at carrying capacity was calculated as:

$$[3.7] \quad b^K = \left[\sum_{A=1}^{\omega} \left(m_{A-1} \prod_{a=1}^A s_a \right) \right]^{-1}$$

It has been suggested that z should be ≥ 1 for marine mammal populations (Fowler 1981, Taylor and DeMaster 1993). I fixed z at 1 (i.e., a linear decrease in birth rate with population size) based on the suggestion of an international working group that harbour porpoise may be relatively more ‘ r -selected’ than other cetaceans (IWC 2000). A higher value of z produces a higher maximum net productivity level and

allows the population to sustain a higher absolute amount of bycatch under equilibrium conditions. Theoretically it would have been possible to estimate z , but the data contained very little information about density-dependence so the estimation of z would likely have been highly confounded with estimates of other parameters (e.g., maximum birth rate, carrying capacity).

I could also have explored a model with density-dependent survival rates. It has been suggested that juvenile survival rate might be the first vital rate to be affected by changes in the density of marine mammal populations (Eberhardt 1977). However, given the lack of information contained in the data about density-dependence my main objective was simply to consider a density-dependent model rather than to determine the precise mechanism by which density-dependence might operate.

After reproduction, simultaneous natural and bycatch mortalities were applied for the remainder of the year:

$$[3.8] \quad N_{a,i,t+1} = N_{a,i,t+0.5} e^{-\left(\frac{M_a + F_{a,i,t}}{2}\right)}$$

Dispersal among subpopulations was assumed to occur at the end/beginning of the year:

$$[3.9] \quad N_{a,i,t} = N_{a,i,t} - \delta_i N_{a,i,t} + \sum_j^{j \neq i} N_{a,j,t} \frac{\delta_j}{I-1}$$

where δ_i is the rate of dispersal from subpopulation i (estimated or fixed) and I is the total number of subpopulations. Eq. 3.9 assumes that animals of all ages disperse at the same rate and that dispersing animals enter other subpopulations with equal probability.

The density-independent population model was initialised by estimating the total number of females alive at the beginning of the first year, $\sum_{a=0}^{\omega} N_{a,i,0}$, and assuming the stable age distribution at the beginning of a year specified by Eqs 3.1-3.5 and 3.8 with effort in each fishery set to the effort in the first year (dominant eigenvector of the transition matrix adjusted for mortality in the latter half of a year). I used the stable age distribution with fishing mortality because there was substantial fishing effort

prior to my study period. In reality, a stable age distribution would not occur, but it is a useful approximation that avoids having to estimate the initial age structure as separate parameters (e.g., Wade 2002b).

The density-dependent population model was initialised by estimating the total number of female non-calves alive at the beginning of the first year, $\sum_{a=1}^{\omega} N_{a,i,0}$, (Wade 2002b) and assuming the stable age distribution at the beginning of a year under density-independent growth with the initial birth rate. I could have estimated the population status in the first year (number of non-calves as a proportion of carrying capacity) rather than the number of non-calves. However, a preliminary analysis indicated that the estimation of initial population status was difficult because of its correlation with carrying capacity. It would not have been necessary to estimate this additional parameter of the density-dependent model if it was assumed that the population was at carrying capacity at the beginning of the study period. However, because of the limited temporal coverage of the available fishing effort data, I was unable to model bycatch and population dynamics from a point in time at which the population was likely at carrying capacity.

In my basic model, the only calf mortality that results from bycatch (Eqs 3.1-3.3 and 3.8) is calves that are directly bycaught according to their age-specific vulnerability. However, if lactating females with dependent calves are bycaught then their abandoned calves will die, but potentially not be part of the bycatch. I considered a scenario with calf abandonment where calves were subject to additional mortality equal to their mother's bycatch mortality rate. Eq. 3.1 was thus modified for age 0 animals:

$$[3.10] \quad N_{1,i,t+0.5} = \sum_{a=1}^{\omega} N_{0/a,i,t} e^{-\left(\frac{M_0 + F_{0,i,t} + F_{a,i,t}}{2}\right)}$$

where $N_{0/a,i,t}$ is the number of calves with mothers of age a in subpopulation i at the beginning of year t . Eq. 3.8 was modified similarly. Eq. 3.10 assumes that calves are entirely dependent on their mothers for their first year of life (i.e., the calf of a bycaught mother will die) and that the probability of a calf being bycaught is independent of the probability of the mother being bycaught. Similar assumptions

were made by Woodley (1993) in a modelling study of dolphin bycatch. The latter assumption seems unlikely because mothers and calves would be together and thus experience similar risks of bycatch. Nevertheless, I modelled this scenario as the maximum possible abandonment of calves as a result of bycatch.

Data

Study area

My study area was the North Sea and adjacent waters (Fig. 3.1). The southwestern boundary of my study area was the western boundary of the International Council for the Exploration of the Sea (ICES) Division VIIId. The northwestern and northern boundaries of my study area were the western and northern boundaries of ICES Division IVa excluding the northwest-most corner for which abundance estimates were not available. The eastern boundary of my study area was the eastern boundary of the North Sea as defined in Vinther (1999). I defined my study period as the years 1987-2005. While there was substantial gillnet fishing effort in the North Sea prior to the late 1980s, detailed effort data were not available for years before 1987 for all fisheries. Thus, I did not extend the study period further back in time.

I considered two different population structures for modelling. For the first structure I assumed that all of the harbour porpoise in the North Sea comprised a single, panmictic population. For the second structure I assumed that the North Sea population was composed of two hypothetical subpopulations, a northern subpopulation and a southern subpopulation, with adjacent and non-overlapping geographic ranges (Walton 1997). The division between the northern and southern subpopulations was assumed to be at 56°N between the east coast of the UK and 7°E, and at 55.5°N between 7°E and the west coast of Denmark. The range of the northern subpopulation corresponded to ICES statistical rectangles ≥ 41 and 40F7 and 40F8. The division between the northern and southern subpopulations was chosen to correspond with the division between survey strata for available abundance data.

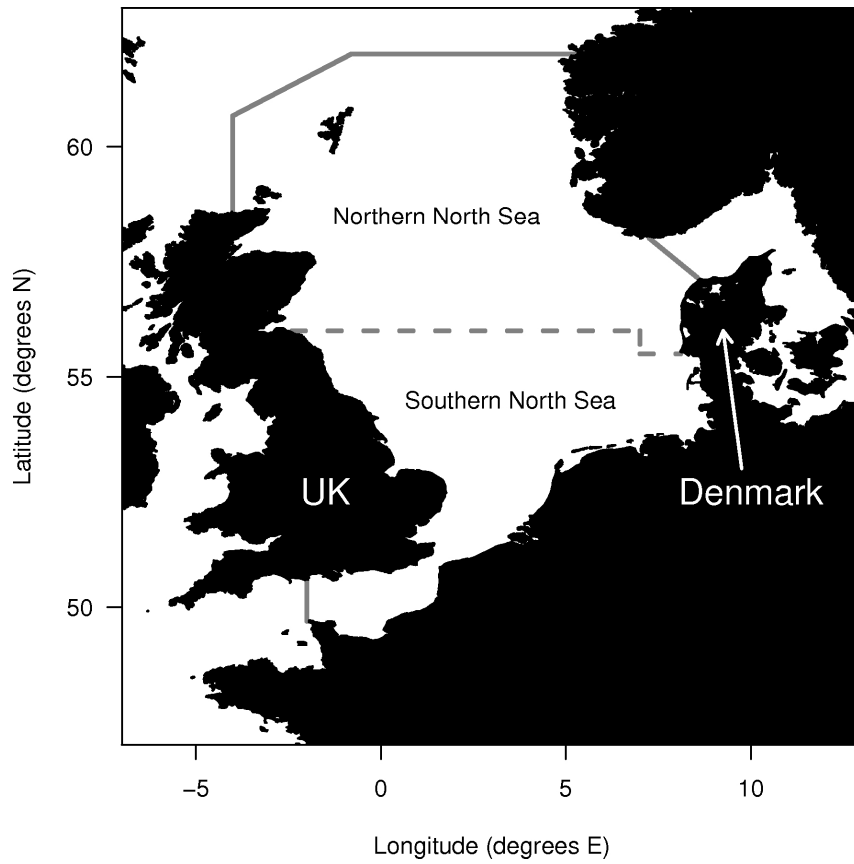


Figure 3.1. Map of the study area (enclosed by solid grey lines). The dashed line indicates the division between the ranges of hypothetical northern and southern subpopulations.

Abundance

Data on abundance of harbour porpoise in the North Sea were available from the Small Cetaceans of the European Atlantic and North Sea (SCANS) and SCANS-II double-platform line-transect surveys (Hammond et al. 2002, SCANS-II 2008). These ship and aerial surveys took place in late June and July of 1994 and 2005, respectively. Mean abundance estimates for the entire study area and for the northern and southern sub-areas were derived using spatial density models fitted to the line-transect data for the entire survey (Hedley and Buckland 2004, Louise Burt and Charles Paxton pers. comm.). CVs were estimated from 1000 non-parametric bootstrapped estimates with transects as sample replicates. The abundance estimates for the entire study area in 1994 and 2005 were 265,606 (CV=0.16) and 216,415 (0.20), respectively. The abundance estimates for the northern sub-area in 1994 and 2005 were 190,028 (0.17) and 91,175 (0.22) and the abundance estimates for the southern sub-area were 75,578 (0.20) and 125,240 (0.21). These abundance estimates were within 10% of approximate estimates derived by summing design-based estimates except for the southern North Sea estimate for 1994, which was about 25% higher than the approximate estimate.

Life History

Data on age at sexual maturity, pregnancy rate and the age structure of female harbour porpoises dying from bycatch and natural causes were available from specimens that stranded along the North Sea coasts of the UK and Denmark and specimens that were bycaught in UK and Danish fisheries in the North Sea (Tables 3.1 and 3.2). A UK-wide Marine Mammal Strandings Programme, coordinated by the Institute of Zoology and Natural History Museum (London) and Scottish Agricultural College (Inverness), has been recovering the carcasses of harbour porpoises that have stranded or been caught in fishing nets around the UK coast since 1990. Researchers in Denmark have been recovering stranded, bycaught and directly caught specimens as far back as the mid-1800s and data on these animals are contained in a central database administered by the National Institute of Aquatic Resources.

Table 3.1. Number of females by age, country, sexual maturity status, and mortality type (natural and bycatch). Data on natural mortality were not available for Denmark because probable cause of death was not established for stranded animals. Data are summarized for all years, but the model was fitted to mortality data from each year separately.

Age	Sexual maturity				Natural mortality	Bycatch mortality	
	UK		Denmark		UK	UK	Denmark
	No	Yes	No	Yes			
0	46	0	16	0	32	12	4
1	36	0	8	1	23	13	12
2	18	0	3	0	14	4	4
3	11	1	3	6	9	5	9
4	9	6	2	2	14	3	2
5	3	10	2	3	8	4	1
6	0	8	1	2	6	4	2
7	0	5	0	3	4	2	0
8	0	6	0	3	5	2	2
9	0	6	1	2	5	1	1
10	0	3	0	3	2	1	1
11	0	4	0	1	3	1	1
12	0	6	0	1	3	2	1

Table 3.1 contd.

Age	Sexual maturity				Natural mortality	Bycatch mortality	
	UK		Denmark		UK	UK	Denmark
	No	Yes	No	Yes			
13	0	1	0	1	1	0	0
14	0	2	0	1	1	1	1
15	0	1	0	2	0	1	1
16	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0
18	0	1	0	0	1	0	0
19	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0
21	0	0	0	1	0	0	0
22	0	1	0	0	1	0	0

Table 3.2. Number of sexually mature females by pregnancy status, year, country, and health status. Animals whose probable cause of death was trauma (e.g., bycatch, bottlenose dolphin attack) were considered healthy. Years represent 1 September-31 May. Data from June-August were not considered because of the possibility that early-term fetuses were missed during examination.

Year	UK				Denmark			
	All		Healthy		All		Healthy	
	No	Yes	No	Yes	No	Yes	No	Yes
1986/1987	0	0	0	0	0	1	0	0
1987/1988	0	0	0	0	0	0	0	0
1988/1989	0	0	0	0	0	0	0	0
1989/1990	0	0	0	0	1	0	0	0
1990/1991	1	0	0	0	0	0	0	0
1991/1992	1	1	1	0	0	0	0	0
1992/1993	0	1	0	0	2	0	2	0
1993/1994	0	0	0	0	0	0	0	0
1994/1995	3	1	1	0	1	0	0	0
1995/1996	0	1	0	1	0	0	0	0
1996/1997	3	2	1	0	0	0	0	0
1997/1998	6	1	1	0	0	4	0	4

Table 3.2 contd.

Year	UK				Denmark			
	All		Healthy		All		Healthy	
	No	Yes	No	Yes	No	Yes	No	Yes
1998/1999	4	2	0	0	1	0	0	0
1999/2000	2	2	0	1	0	0	0	0
2000/2001	0	2	0	2	0	0	0	0
2001/2002	2	1	0	1	0	2	0	0
2002/2003	5	3	0	1	0	0	0	0
2003/2004	1	0	0	0	0	0	0	0
2004/2005	1	0	1	0	0	0	0	0

Detailed post-mortem examinations were undertaken on many of these carcasses to determine *inter alia* age, sexual maturity, pregnancy and probable cause of death (Clausen and Andersen 1988, Sørensen and Kinze 1994, Jepson 2003, Learmonth 2006). Age was determined by counting growth layer groups in the dentine of decalcified tooth sections. A few ages were minimum estimates. Sexual maturity was established using gonadal appearance and the presence of at least one corpus luteum or corpus albicans. For this study I considered pregnancy to be established by the presence of a foetus. For specimens from England and some specimens from Scotland, pregnancy was established by the mention of a foetus in post-mortem reports. No mention of a foetus was interpreted as not pregnant, unless it appeared that a detailed post-mortem examination had not been done (in which case reproductive status was assumed to be unknown). I did not consider data on pregnancy from the months of June-August because of a potentially lower probability of detection of early-term foetuses (Van Utrecht 1978, Read 1990a, Sørensen and Kinze 1994, Lockyer 1995b, Börjesson and Read 2003, Learmonth 2006). In the UK data, the probable cause of death of stranded animals was classified using several categories, but for the purpose of this study I categorized probable cause of death as bycatch or 'natural' (the latter including mainly physical trauma other than bycatch, disease and starvation/hypothermia). More than 2/3 of the 'bycaught' animals in the UK data were stranded specimens that were diagnosed as dying as a result of bycatch. In the Danish data, specimens were classified as stranded or directly bycaught. I only used age-structure data from directly bycaught animals from Denmark because the strandings data could not be split by cause of death. I also categorized animals as 'healthy' or not with the former category containing bycaught animals and stranded animals whose probable cause of death was bycatch or other physical trauma (Jepson 2003).

I used life history data on specimens from ICES Sub-area IV and Division VIIId and the coasts of the UK and Denmark within my study area during the years 1986-2005. For the two-subpopulation model I split the data into two groups corresponding to the geographic ranges of the subpopulations. However, not all of the data had detailed enough locations to allocate them to a specific subpopulation, thus fewer data on pregnancy and age structure of bycatch mortality were used to fit the two-subpopulation model. The sample size of pregnancy data was reduced from 58 to 52

and the sample size of bycatch age structure was reduced from 98 to 78. It is possible that some of the stranded specimens originated outside my study area or from the opposite subpopulation to which they were assigned because of the drift of carcasses at sea.

Bycatch and fishing effort

Data on bycatch rate and total fishing effort were available for UK and Danish fisheries in the North Sea. I considered five UK-registered North Sea ‘fisheries’ in which bycatch was observed. Fisheries were defined by the fish species that comprised the greatest value in the catch from a fishing trip: cod/gadoid (not hake), sole (*Solea solea*), skate (Rajidae), turbot (*Psetta maxima*) and offshore wreck-net fishery (Northridge et al. 2007). The last fishery was defined based on home port (Grimsby), vessel length and target species—most of the catch in this fishery was cod. The effort in these five fisheries was mostly concentrated in ICES Division IVc and the southwest quadrant of Division IVb, however, there was also effort in the northern North Sea around the Orkney and Shetland Islands. Data from a UK observer programme (1996-2004) were used to estimate bycatch per unit effort for each of these fisheries (Northridge et al. 2003, Northridge et al. 2007). Each of the five selected fisheries had observed effort for one or more years between 1996 and 2004 (Table 3.3). Data were available on the number of hauls observed in each fishery during a given year and the number of harbour porpoise observed bycaught. Data were also available on total fishing effort for each year and fishery as days at sea. Days at sea were converted to estimated number of hauls for each year and fishery ($E_{h,i,t}$) using the observed average number of hauls per day in each fishery from the observer programme (Table 3.4).

I considered five Danish bottom-set gillnet fisheries in the North Sea in which bycatch was observed: cod-wreck, cod-other, hake (*Merluccius merluccius*), turbot (*Scophthalmus rhombus*) and plaice (*Pleuronectes platessa*). These fisheries were defined based on a cluster analysis of the relative landings value of common species landed (Vinther 1999). Fishing effort was distributed throughout ICES Sub-area IV, but most effort occurred in the eastern half of Division IVb (Vinther 1999). Data from a Danish observer programme (1993-2001) were used to estimate bycatch per unit

Table 3.3. Data on observed fishing effort and bycatch by country and fishery.

Year	UK										Denmark									
	Observed effort (number of hauls)					Observed number of porpoise bycaught					Observed effort (target species landings in t)					Observed number of porpoise bycaught				
	Cod-wreck	Cod/gadoid	Skate	Sole	Turbot	Cod-wreck	Cod/gadoid	Skate	Sole	Turbot	Cod-wreck	Cod-other	Hake	Plaice	Turbot	Cod-wreck	Cod-other	Hake	Plaice	Turbot
1993	0	0	0	0	0	0	0	0	0	0	49.4	113	0	0.084	10.1	25	46	0	0	46
1994	0	0	0	0	0	0	0	0	0	0	47.4	4.30	0	5.12	8.95	2	0	0	1	39
1995	0	0	0	0	0	0	0	0	0	0	10.2	2.73	0	0	0	0	2	0	0	0
1996	182	322	0	4	44	0	1	0	0	1	13.1	30.0	0	9.83	5.05	0	7	0	3	11
1997	398	903	24	102	29	8	8	0	1	1	46.8	103	3.07	3.77	5.80	8	19	4	0	58
1998	139	1089	61	132	0	1	2	4	0	0	11.9	2.31	0	32.2	0.643	0	31	0	17	1
1999	0	97	17	34	0	0	0	0	1	0	0	0	0	14.9	0.100	0	0	0	0	0
2000	0	49	141	74	43	0	2	9	1	0	4.20	11.9	0	2.82	0	0	9	0	0	0
2001	0	56	88	28	0	0	0	4	0	0	0	0	0	1.58	0	0	0	0	0	0
2002	0	31	225	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0
2003	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2004	0	0	286	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0

Table 3.4. Data on total fishing effort by country and fishery.

Year	UK (estimated number of hauls)					Denmark (estimated target species landings in t)				
	Cod-wreck	Cod/gadoid	Skate	Sole	Turbot	Cod-wreck	Cod-other	Hake	Plaice	Turbot
1987	8063	42352	796	10792	305	3486	3486	89	1574	536
1988	7156	37588	706	9578	271	3781	3781	119	1287	637
1989	8140	42757	804	10895	308	3443	3443	158	783	498
1990	9063	47608	895	12131	343	3458	3458	200	884	603
1991	12056	54857	1513	11697	550	3644	3644	303	3441	603
1992	14972	57255	2722	14560	545	4295	4295	406	3972	509
1993	15362	57155	2012	14689	227	4720	4720	522	3441	443
1994	14345	43648	3552	13090	973	4821	4821	369	5511	500
1995	12856	46344	3655	19745	277	4666	4666	285	4487	467
1996	13307	41506	2343	14298	610	4588	4588	143	4373	395
1997	12000	39874	2045	19040	187	5107	5107	90	3458	276
1998	8729	47291	1090	14044	252	5958	5958	106	2154	204
1999	9484	25831	1529	15940	459	4816	4816	163	1765	147
2000	6836	20469	1361	13056	419	4355	4355	135	1615	196
2001	7220	13507	1074	14307	514	2836	2836	118	3062	228
2002	3220	14485	1573	11775	620	3007	3007	127	2414	285
2003	2836	10655	1388	13473	479	1485	1485	178	2580	170
2004	2567	5493	1719	9281	338	2181	2181	169	2425	196
2005	1625	2880	1537	13137	318	2276	2276	194	2284	100

effort for each of these fisheries (Vinther and Larsen 2004). Each of the five selected fisheries had observed effort for one or more years between 1993 and 2001 (Table 3.3). Data were available on the target species landings observed in each fishery during a given year and the number of harbour porpoise observed bycaught. Data were also available on total fishing effort for each year and fishery as days at sea. Days at sea were converted to estimated landings for each year and fishery ($E_{h,i,t}$) using the average total target species landings per day in each fishery during the years of the observer programme (Table 3.4). This approach is equivalent to the ‘effort’ method of Vinther and Larsen (2004) which uses estimated total landings rather than reported total landings, and assumes constant catch-per-unit-effort during the years of the observer programme.

The majority of fishing effort was in my southern North Sea area: >90% of effort in all UK fisheries, and about 70-90% of effort in Danish fisheries except turbot which was evenly split between the northern and southern sub-areas. The majority of observed effort for UK fisheries was also in the southern sub-area. However, the distribution of observed effort varied among Danish fisheries with some having more observed effort in the northern sub-area (cod-wreck, plaice, turbot) and some having more in the south (cod-other, hake). The total observed fishing effort during 1987-2005 represented 0.4% and 0.3% of the estimated total fishing effort for the UK and Denmark, respectively. Observer coverage for individual UK fisheries in years with observer effort ranged from 0.03-17% (median=1%) and for Danish fisheries ranged from 0.002-3% (median=0.3%).

Fishing effort was not distributed evenly throughout the year and there is evidence that bycatch rates varied seasonally (Vinther and Larsen 2004). However, for simplicity I assumed that the annual effort for each fishery was distributed uniformly throughout the year and that the rate of bycatch per unit effort per porpoise density was constant.

It is important to note that I did not consider all North Sea fisheries in my analysis. There are several UK (dogfish, monkfish and herring) and Danish fisheries (sole) that had observer effort during my study period, but had no observed bycatch of harbour porpoise. In a preliminary analysis I attempted to fit the model to data from these fisheries in addition to data from fisheries in which bycatch was observed. The

statistical framework that I used allows for estimation of a non-zero probability of bycatch in fisheries where no bycatch was observed (Razzaghi 2002). However, because only small proportions of the total effort in these fisheries were observed there was little information in the data about bycatch rates in these fisheries. Thus, the estimation of these rates was relatively unconstrained and problematic. To avoid these difficulties in model fitting, these fisheries were ignored (i.e., assumed to have no bycatch).

Parameter estimation

Parameters of the population model were estimated using a Bayesian statistical framework (Table 3.5). Six likelihood functions related the data to the model.

Errors in estimates of abundance were assumed to be log-normally distributed:

$$[3.11] \quad L^N = \prod_{i=1}^I \prod_t \frac{1}{x_{i,t}^N \sigma_{i,t} \sqrt{2\pi}} e^{-\frac{\left[\log(x_{i,t}^N) - \log\left(2 \sum_{a=0}^{\omega} N_{a,i,t+0.5}\right) \right]^2}{2\sigma_{i,t}^2}}$$

where L^N is the likelihood of the abundance data, $x_{i,t}^N$ is the mean abundance estimate for subpopulation i in year t and $\sigma_{i,t}$ is the standard deviation of the errors on a log-scale which was calculated from the coefficients of variation according to:

$$[3.12] \quad \sigma_{i,t} = \sqrt{\log(1 + CV_{i,t}^2)}$$

Eq. 3.11 assumes a 1:1 sex ratio and that surveys were conducted at mid-year immediately after births.

The proportion of females that was sexually mature at a given age was assumed to be binomially distributed:

$$[3.13] \quad L^M = \prod_{a=0}^{\omega} \binom{n_a^M}{x_a^M} (m_{a+0.5})^{x_a^M} (1 - m_{a+0.5})^{n_a^M - x_a^M}$$

Table 3.5. Estimated parameters of the population model. Prior probability distributions were uniform (described by a lower limit and an upper limit).

Symbol	Description	# of parameters	Prior probability distribution
$\sum_{a=0}^{\omega} N_{a,i,0}$	initial number of females (density-independent)	$1 \times I$	0, 500000
$\sum_{a=1}^{\omega} N_{a,i,0}$	initial number of female non-calves (density-dependent)	$1 \times I$	0, 500000
$N_i^{1+,K}$	number of female non-calves at carrying capacity (density-dependent)	$1 \times I$	0, 500000
a^{m50}	age when 50% of females are mature	1	2, 6
σ^m	width of maturity ogive	1	0, 2
b_i	birth rate (density-independent)	$1 (\times I)$	0, 0.5
b^{\max}	maximum birth rate (density-dependent)	1	0, 0.5
s_a	natural age-specific survival	4	0, 1
η_a	age-specific vulnerability to bycatch	3	0, 10
q_h	bycatch per unit effort in fishery h	10	0, 1

Table 3.5 contd.

Symbol	Description	# of parameters	Prior probability distribution
δ_i	dispersal rate from northern subpopulation (Scenario 8)	1	0, 1
δ_i	dispersal rate from northern subpopulation (Scenario 9 – linear increase, first t (1987) = 0)	2	intercept: 0, 0.2 slope: 0, 1
θ	overdispersion of beta-binomial likelihood	1	1e-10, 1e10

where L^M is the likelihood of the sexual maturity data, n_a^M is the total number of females of age a (all subpopulations) that were sampled and examined for sexual maturity and x_a^M is the number of those females that was sexually mature. Eq. 3.13 assumes that the overall proportion of females of a given age that is mature is equal to the probability of being mature at the mid-point of that year of life. The sexual maturity ogive was assumed to be identical among subpopulations.

I assumed that the birth rate ($b_{i,t}$) was equal to half the proportion of mature females that was pregnant (i.e., 1:1 sex ratio at birth) which was assumed to be binomially distributed:

$$[3.14] \quad L^P = \prod_{i=1}^I \prod_t \binom{n_{i,t}^P}{x_{i,t}^P} (2b_{i,t})^{x_{i,t}^P} (1-2b_{i,t})^{n_{i,t}^P - x_{i,t}^P}$$

where L^P is the likelihood of the pregnancy data, $n_{i,t}^P$ is the total number of sexually mature females in subpopulation i sampled in the last half of year $t-1$ and the first half of year t that were examined for pregnancy and $x_{i,t}^P$ is the number of those females that was pregnant. Eq. 3.14 assumes no prepartum mortality of foetuses; the occurrence of prepartum resorptions or abortions of foetuses would cause birth rate to be positively biased. Eq. 3.14 also assumes that sampling errors in pregnancy rate are independent among subpopulations and years. Unmodelled variability in birth rate among subpopulations or years or non-random sampling of mature females (e.g., sampling of a single group of females in a given year with similar probabilities of pregnancy) could have resulted in non-independence and overdispersion of the data relative to a binomial likelihood function. I explored the use of a beta-binomial likelihood to estimate overdispersion in the pregnancy data, but the posterior for the overdispersion parameter suggested that there was none. This was a result of the small sample sizes for the pregnancy data. Reducing the effective sample sizes further by allowing for overdispersion did not increase the likelihood of the data.

The proportions of total natural mortality composed of females of each age were assumed to be multinomially distributed:

$$[3.15] \quad L^{\text{DNat}} = \prod_{i=1}^I \prod_t \left(\frac{\sum_{a=0}^{\omega} x_{a,i,t}^{\text{DNat}}!}{x_{0,i,t}^{\text{DNat}}! x_{1,i,t}^{\text{DNat}}! \dots x_{\omega,i,t}^{\text{DNat}}!} \right) \prod_{a=0}^{\omega} (d_{a,i,t}^{\text{Nat}})^{x_{a,i,t}^{\text{DNat}}}$$

where L^{DNat} is the likelihood of the natural mortality data, $d_{a,i,t}^{\text{Nat}}$ is the proportion of total natural mortality in subpopulation i in year t composed of females of age a and $x_{a,i,t}^{\text{DNat}}$ is the number of females of age a in subpopulation i sampled in year t whose probable cause of death was natural. The proportion of total natural mortality composed of females of a given age in a given subpopulation in a given year was calculated according to the following two equations:

$$[3.16] \quad d_{a,i,t}^{\text{Nat}} = \frac{D_{a,i,t}^{\text{Nat}}}{\sum_{a=0}^{\omega} D_{a,i,t}^{\text{Nat}}}$$

and

$$[3.17] \quad D_{a,i,t}^{\text{Nat}} = (N_{a,i,t} + N_{a,i,t+0.5}) \left[1 - e^{-\left(\frac{M_a + F_{a,i,t}}{2}\right)} \right] \frac{M_a}{M_a + F_{a,i,t}}$$

where $D_{a,i,t}^{\text{Nat}}$ is the number of females of age a in subpopulation i dying of natural mortality in year t . Note that in the scenario where calves died from abandonment, the abandoned calves were added to $D_{0,i,t}^{\text{Nat}}$ because these calves could potentially strand after dying but would not exhibit signs of bycatch:

$$[3.18] \quad D_{0,i,t}^{\text{Nat}} = \sum_{a=1}^{\omega} (N_{0/a,i,t} + N_{0/a,i,t+0.5}) \left[1 - e^{-\left(\frac{M_a + F_{0,i,t} + F_{a,i,t}}{2}\right)} \right] \frac{M_a + F_{a,i,t}}{M_a + F_{0,i,t} + F_{a,i,t}}$$

The likelihood of the bycatch mortality age-structure data was calculated in the same way as for natural mortality:

$$[3.19] \quad L^{\text{DByc}} = \prod_{i=1}^I \prod_t \left(\frac{\sum_{a=0}^{\omega} x_{a,i,t}^{\text{DByc}}!}{x_{0,i,t}^{\text{DByc}}! x_{1,i,t}^{\text{DByc}}! \dots x_{\omega,i,t}^{\text{DByc}}!} \right) \prod_{a=0}^{\omega} (d_{a,i,t}^{\text{Byc}})^{x_{a,i,t}^{\text{DByc}}}$$

$$[3.20] \quad d_{a,i,t}^{\text{Byc}} = \frac{D_{a,i,t}^{\text{Byc}}}{\sum_{a=0}^{\omega} D_{a,i,t}^{\text{Byc}}}$$

$$[3.21] \quad D_{a,i,t}^{\text{Byc}} = (N_{a,i,t} + N_{a,i,t+0.5}) \left[1 - e^{-\left(\frac{M_a + F_{a,i,t}}{2}\right)} \right] \frac{F_{a,i,t}}{M_a + F_{a,i,t}}$$

The total mortality rate in Eq. 3.21 was altered as shown in Eq. 3.18 to account for calf abandonment in that scenario.

As with the likelihood for the pregnancy data, Eqs 3.15 and 3.19 assumed that sampling errors in mortality age structure were independent among subpopulations and years. Unmodelled heterogeneity in age structure of mortality among subpopulations or years or non-random sampling of animals (e.g., bycatch of groups of females with different age structures) could have resulted in non-independence and overdispersion of the data relative to a multinomial likelihood function. I explored the use of a Dirichlet-multinomial likelihood to estimate overdispersion in the age structure data, but as with the pregnancy data, the estimated overdispersion was negligible as a result of the already small sample sizes. An alternative approach would have been to effectively reduce the sample sizes by a fixed factor (Hoyle and Maunder 2004), however given the results with the Dirichlet-multinomial likelihood I did not feel that this was appropriate.

The proportion of the total bycatch that was observed was assumed to be beta-binomially distributed:

$$[3.22] \quad L^{\text{Byc}} = \prod_{h=1}^H \prod_{i=1}^I \prod_t \frac{\binom{n_{h,i,t}^{\text{Byc}}}{x_{h,i,t}^{\text{Byc}}} \text{Beta} \left[x_{h,i,t}^{\text{Byc}} + \theta \frac{E_{h,i,t}^{\text{Obs}}}{E_{h,i,t}}, n_{h,i,t}^{\text{Byc}} - x_{h,i,t}^{\text{Byc}} + \theta \left(1 - \frac{E_{h,i,t}^{\text{Obs}}}{E_{h,i,t}} \right) \right]}{\text{Beta} \left[\theta \frac{E_{h,i,t}^{\text{Obs}}}{E_{h,i,t}}, \theta \left(1 - \frac{E_{h,i,t}^{\text{Obs}}}{E_{h,i,t}} \right) \right]}$$

where L^{Byc} is the likelihood of the bycatch data, $n_{h,i,t}^{\text{Byc}}$ is the predicted number of animals bycaught in fishery h from subpopulation i in year t , $x_{h,i,t}^{\text{Byc}}$ is the observed number of animals bycaught in the range of subpopulation i , $E_{h,i,t}^{\text{Obs}}$ is the number of

hauls (UK) or landings (Denmark) observed in fishery h in the range of subpopulation i during year t , θ is a parameter used to model overdispersion relative to a binomial likelihood (smaller values of θ result in more overdispersion so as θ approaches infinity the beta-binomial distribution becomes equivalent to the binomial distribution), and $\text{Beta}()$ is the mathematical beta function. The predicted numbers of animals (male and female) bycaught in each fishery each year were calculated according to:

$$[3.23] \quad n_{h,i,t}^{\text{Byc}} = \frac{q_h E_{h,i,t}}{\sum_{h=1}^H q_h E_{h,i,t}} 2 \sum_{a=0}^{\omega} D_{a,i,t}^{\text{Byc}}$$

and then rounded to the nearest integer for use in Eq. 3.22. It was ensured that the likelihood in Eq. 3.22 was zero if the observed bycatch was greater than the predicted bycatch. It was also ensured that if all effort was observed, the only non-zero likelihood occurred when predicted bycatch equalled observed bycatch. Eq. 3.23 assumes a 1:1 sex ratio.

It is important to note that I estimated total bycatch by fitting my population model to data on bycatch rate and inputting data on ‘known’ total fishing effort (Pout et al. 2001). This differs from the more common approach of estimating total bycatch independently and then inputting these estimates of mortality to the model. Estimating bycatch within the model fitting framework ensured consistency in inference.

The six likelihoods (Eqs 3.11, 3.13, 3.14, 3.15, 3.19, 3.22) were assumed to be independent (i.e., independent random sampling errors) so that the total likelihood was the product of the individual likelihoods. Likelihoods with shared unknown parameters and/or random observables are potentially not independent and failing to account for dependence can result in overly precise posterior probability intervals (Goodman 2004). The likelihoods for the sexual maturity ogive and birth rate (Eqs 3.13 and 3.14) did not share any unknown parameters and thus were independent from each other. However, all other combinations of likelihoods implicitly share unknown parameters through the population dynamics equations. The likelihood for absolute abundance (Eq. 3.11) did not share any random observables with any of the other likelihoods and was therefore independent. However, the other five likelihoods

contained design parameters (e.g., sample size) and random observables (e.g., numbers of animals of different sexual maturity statuses, pregnancy statuses and age) that were derived in part from the same sample of specimens. For example, data from the sample of bycaught animals entered into four likelihoods (Eqs 3.13, 3.14, 3.19 and 3.22). Nevertheless, none of the random observables in any of the likelihoods were functions of the random observables in other likelihoods. Random observables were only related to the sample sizes in other likelihoods (design parameters) which is not an issue with respect to independence (Goodman 2004). For example, a change in the total number of animals observed bycaught (the random observable in Eq. 3.22) could potentially change the sample sizes for sexual maturity, pregnancy rate and age structure, but it would not necessarily change the numbers of animals that were sexually mature, pregnant or of a specific age (the random observables in Eqs 3.13, 3.14 and 3.19, respectively). Similarly, a change in the observed age structure of a mortality sample (random observables in Eqs 3.15 and 3.19) could change the number of animals of each age (sample size in Eq. 3.13) or the number of mature animals (sample size in Eq. 3.14) but it would not necessarily change the number of animals of each age that were sexually mature (random observable in Eq. 3.13) or the number of mature animals that were pregnant (random observable in Eq. 3.14). Although sampling errors should have been statistically independent among the different datasets, there was still potential for sampling biases if the life history and age structure of stranded and bycaught animals were not representative of the entire population.

Posterior probability distributions for the parameters of the population model were estimated using a Markov chain Monte Carlo (McMC) algorithm with a Metropolis acceptance/rejection rule (Gelman et al. 2004). McMC is a numerical simulation method for deriving samples from a target distribution when it is not possible to directly sample from that distribution (e.g., it is unknown). In each iteration of the Metropolis algorithm, a change is proposed for the value of a parameter (or set of values for a set of parameters) by randomly drawing a new value from a proposal distribution that is symmetric about the current value. The change is accepted with probability proportional to the ratio of the density of the target distribution for the new parameter value to the density of the target distribution for the previous parameter

value. Over time the chain of parameter values converges to a sample from the target distribution, in this case the posterior probability distribution.

The density of the posterior probability distribution is proportional to the product of the densities of the joint likelihood and the joint prior probability distribution (Gelman et al. 2004). Prior probability distributions were assumed to be uniform (Table 3.5) so that the acceptance rule operated only on the joint likelihood. In practice, I used log-likelihoods instead of likelihoods for computational ease. The uniform prior for the overdispersion parameter of the beta-binomial likelihood (Eq. 3.22) specified a decreasing prior probability for increasing overdispersion which is common for overdispersion/variance parameters (Gelman et al. 2004, Scollnik 1995). Proposal values were drawn from the proposal distributions for each parameter individually followed by acceptance/rejection after each individual parameter draw. A proposed parameter value was accepted if the difference between the new total log-likelihood and the previous log-likelihood was greater than the log of a random uniform number between 0 and 1. Uniform proposal distributions were used with initial widths of 20% of the starting parameter values. These widths were adjusted during the burn-in period with a target acceptance rate of 40% (Gelman et al. 2004). Widths were increased when the acceptance rate was higher and decreased when the acceptance rate was lower. Draws outside the ranges of the prior probability distributions were assigned zero likelihood. With the density-dependent model further constraints were placed on parameter draws so that $b^K < b^{\max}$ and $\sum_{a=1}^{\omega} N_{a,i,0} \leq N_i^{1+,K}$; parameter draws that did not satisfy these constraints were assigned zero likelihood. These constraints on parameter space altered the uniform priors for some parameters so I present realized priors in my results, which I obtained by running the McMC algorithm without consideration of the data (Punt and Butterworth 1999, Brandon et al. 2007). I assessed the convergence of the sample of the joint posterior using the Bayesian Output Analysis package for R for Windows (Smith 2001) including Raftery and Lewis, Geweke and Heidelberger and Welch diagnostics. The McMC chain was run for 3,000,000 iterations keeping every 200th iteration not including a burn-in of 1,000,000 iterations (posterior sample size = 10,000). When full posterior probability distributions are not presented, medians and 95% intervals of posterior probability are presented as summary statistics.

The population model and McMC algorithm were coded using the C computer language compiled with the free MinGW port (<http://www.mingw.org>) of the GNU GCC compiler (<http://www.gnu.org>) and the free software package R (R Development Core Team 2007).

Model scenarios

Nine qualitatively different scenarios were considered with respect to model structure and the data used to fit the model (Table 3.6). Scenario 1 was a base scenario where I fit a model of a single population with density-independent dynamics to all of the data. Scenarios 2-6 also modelled a single population, but considered pregnancy data from healthy females only, no pregnancy data, calf abandonment, a 50% reduction in bycatch rates in Danish fisheries after 2001, and density dependence, respectively. Scenario 5 was designed to capture additional uncertainty in recent bycatch rates in Danish fisheries because some of these fisheries have changed in recent years (e.g., reduced quotas, use of acoustic alarms) and there are no recent observer data (Finn Larsen, pers. comm.).

Scenarios 7-9 modelled two subpopulations, with the first scenario allowing for different birth rates but no dispersal, and the remaining scenarios allowing for dispersal but only one common birth rate. To explore the observed decrease in abundance in the north and increase in the south, I assumed no dispersal from the southern subpopulation to the northern subpopulation and estimated dispersal from the northern subpopulation to the southern subpopulation in Scenarios 8 and 9. In Scenario 8 the dispersal rate from the north (δ_i) was assumed constant, while in Scenario 9 this dispersal rate was allowed to increase linearly throughout the study period. It was necessary to fix the dispersal rate from the southern subpopulation because estimates of dispersal from both subpopulations would be highly correlated given the data used. I chose to fix dispersal from the south at 0 to simplify the hypotheses being modelled. Although I assumed no dispersal from the south, the results of Scenarios 8 and 9 would be similar to those of scenarios where there is dispersal from the south, except that dispersal from the north would then be higher.

Table 3.6. Modelled scenarios.

Feature	Scenario								
	1	2	3	4	5	6	7	8	9
Number of subpopulations	1	1	1	1	1	1	2	2	2
Pregnancy data ¹	all	healthy	none	all	all	all	all	all	all
Calf abandonment	no	no	no	yes	no	no	no	no	no
Bycatch rate in Danish fisheries	constant	constant	constant	constant	50% lower in 2002-05	constant	constant	constant	constant
Density-dependent birth rate	no	no	no	no	no	yes	no	no	no
Subpopulation-specific birth rate	-	-	-	-	-	-	yes	no	no
Dispersal	-	-	-	-	-	-	no	constant	linear increase

¹Pregnancy data were either from all mature females or from healthy mature females

Results

Convergence

The convergence diagnostics suggested that the McMC simulation converged to approximate the posterior distribution for the estimated parameters. The Raftery and Lewis tests resulted in dependence factors for the samples from the posterior that were very close to 1 for all estimated parameters in all scenarios. The Raftery and Lewis tests did not recommend further thinning or burn-ins (recommended burn-ins were negligible—1 or 2 iterations). The Raftery and Lewis tests suggested that samples of around 10,000 or less were sufficient for inferences about the median and 2.5th and 97.5th quantiles to a precision of 0.01 with a probability of 0.95 (the delta parameter for these tests was set to 0.001). The Geweke p-value was only significant at $\alpha = 0.05$ for one parameter in each of two scenarios (when testing the first 10% of iterations a sample against the last 50%). The vast majority of Heidelberger and Welch stationarity and half-width tests were passed without the discarding of samples; discarding only occurred for one parameter in each of four scenarios and for five parameters in one scenario (in the latter, one parameter failed the stationarity test). Given the results of the Raftery and Lewis and Geweke tests, the entire samples from the posteriors were used for inference. The Heidelberger and Welch half-width tests passed at a precision of 0.1 for catchability parameters and at a precision of 0.01 for all other parameters ($\alpha = 0.05$). There was no substantial serial autocorrelation in the estimates for any parameter in the sample from the posterior, although there was sometimes low but significant autocorrelation in estimates of the bycatch rate for the UK sole fishery. This bycatch rate parameter was often the parameter for which discarding occurred with the Heidelberger and Welch test. The estimated bycatch rate in the UK sole fishery was relatively low and only a small proportion of effort was observed (Tables 3.3 and 3.4), which made the estimation of this parameter more difficult. Estimated quantiles for this parameter differed by at most a few percent from preliminary McMC chains that were only half the final length with half the final thinning rate.

The convergence diagnostics also suggested that the McMC sample approximated the posterior distribution for estimated quantities (total number of females, total female bycatch, birth rate, and proportions of natural and bycatch mortality composed of each

age). The results of the Raftery and Lewis tests were identical to those for the estimated parameters. Significant Geweke p-values occurred for estimated quantities in only two scenarios. Most scenarios had estimated quantities for which the Heidelberger and Welch tests discarded samples, but all passed the stationarity and half-width tests. The half-width tests all passed at a precision of 0.01 except for a few estimated numbers of females and bycatches that were small (<10000), which passed at a precision of 0.1. For all of the single population scenarios, preliminary McMC chains of half the final length with half the final thinning rate resulted in estimates of population growth rate in the absence of bycatch that were very similar to the final estimates. A preliminary McMC chain for Scenario 1 with different starting values also resulted in estimates of population growth rate and bycatch that were very similar to the final estimates.

Density-independent model of single population

Scenario 1

The base scenario examined was a density-independent model of a single population, which was fitted to all of the data. The posterior probability distributions for the estimated parameters of this model were very different from the assumed uniform prior probability distributions and generally had well-defined unimodal shapes (Fig. 3.2), which suggested that the ranges of the priors were appropriate and that the priors did not have a great influence on the posteriors.

The estimated sexual maturity ogive was the only life history feature that closely matched the data (Fig. 3.3). The median estimated age at which 50% of females were sexually mature was 4.5 years with a 95% interval of posterior probability of 3.9-4.9 years, and 90% of females were estimated to be mature by 6.4 (5.7-7.3) years of age. The estimated annual birth rate (0.65, 0.57-0.73 male and female calves per mature female) was much higher than the observed pregnancy rate for the entire sample of mature females (0.41, Fig. 3.4)—an apparent inconsistency between the model and the data. The estimated natural annual survival rate of calves was 0.81 (0.73-0.87) and estimated natural survival rate increased with age to 0.88 (0.83-0.92) for sexually mature females (Fig. 3.2). However, the model underestimated the proportion of natural mortality that was composed of young animals and overestimated the proportion of older animals (Fig. 3.5).

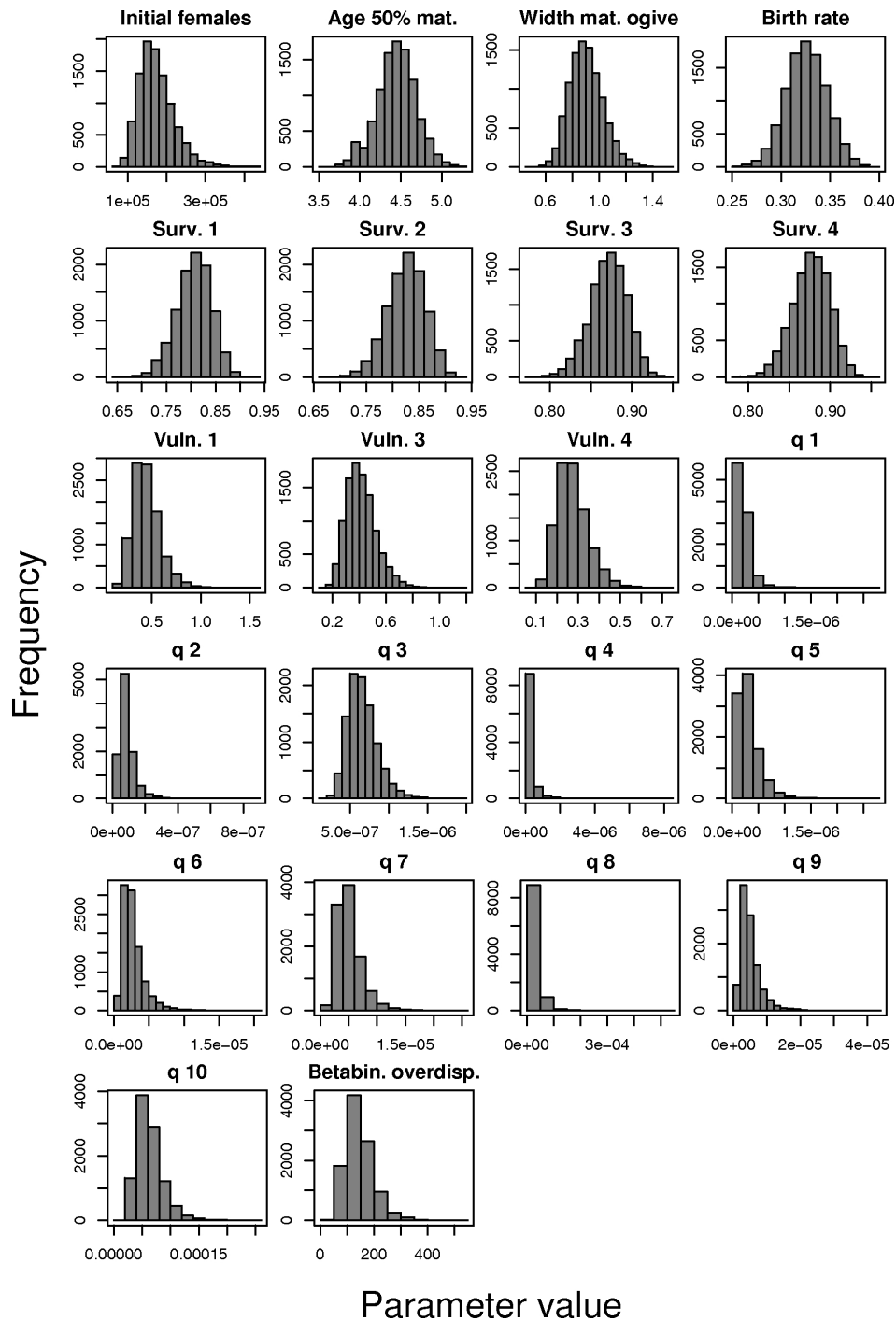


Figure 3.2. Marginal posterior probability distributions of the estimated parameters (Table 3.5) of the density-independent model of a single population (Scenario 1, Table 3.6). Plots are histograms of a sample of 10,000 parameter values from the joint posterior. All marginal prior probability distributions were uniform.

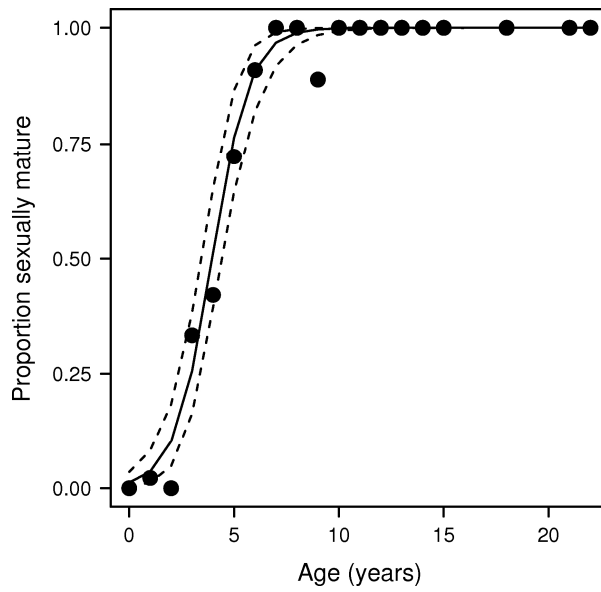


Figure 3.3. Observed (points) and predicted (lines) sexual maturity ogive for the density-independent model of a single population (Scenario 1, Table 3.6). Solid line indicates median values from the posterior sample and dashed lines represent the 95% interval of values from the posterior sample. The x-axis represents the mid-points of the indicated ages.

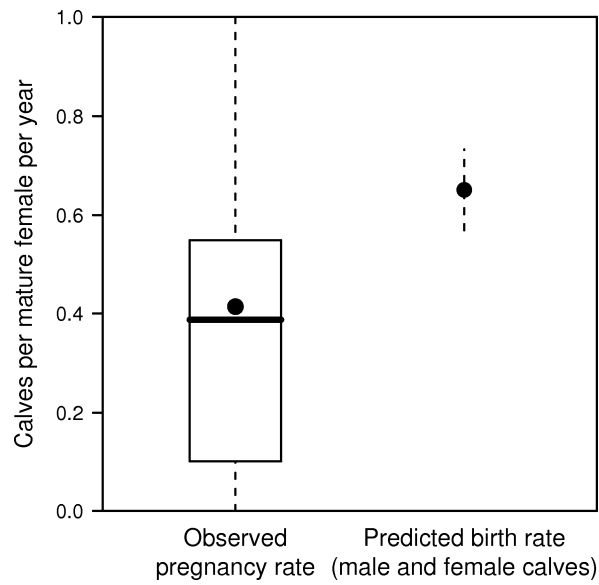


Figure 3.4. Observed pregnancy rate and predicted birth rate for the density-independent model of a single population (Scenario 1, Table 3.6). The boxplot on the left represents the distribution of observed pregnancy rates across years during the study period (point represents the overall pooled pregnancy rate). The data point and dashed line on the right represent the median and 95% interval of predicted values for birth rate (male and female calves) from the posterior sample, respectively.

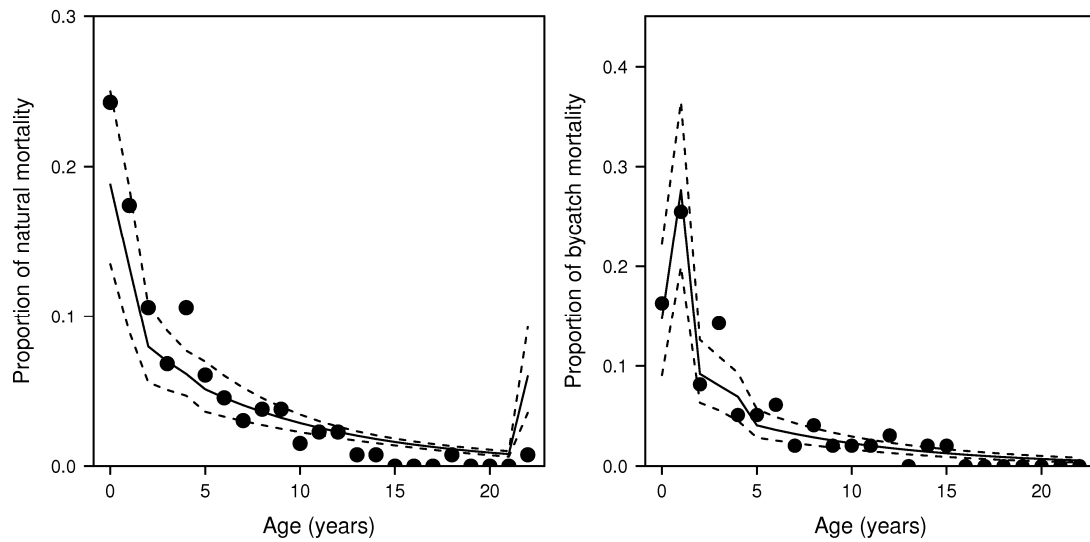


Figure 3.5. Observed (points) and predicted (lines) age structure of natural and bycatch mortality for the density-independent model of a single population (Scenario 1, Table 3.6). Observed values represent overall proportions (data pooled across years) and predicted values represent average proportions across all years of the study period. Solid line indicates median values from posterior sample and dashed lines represent the 95% interval of values from the posterior sample. Note that the model was fitted to the data from individual years separately (Eqs 3.15 and 3.19), not the pooled data presented in this Figure.

Estimated vulnerabilities of calves and females >1 year of age to bycatch were lower than for 1-year-old animals with >95% probability (Fig. 3.2). Mature females had the lowest median estimated vulnerability. These vulnerabilities resulted in an estimated age structure of animals dying from bycatch that was similar to the observed age structure with a distinct peak at 1 year of age (Fig. 3.5). Estimated bycatch for individual fisheries was highly uncertain, but was generally within the range of bycatch calculated directly from annual observed bycatch rates (Fig. 3.6). Estimated bycatch was higher for Danish fisheries than for UK fisheries. Total bycatch was higher during the first half of the study period than during the second half with a maximum median estimate of 11,600 males and females (7,800-19,500) in 1992 and a minimum of 3,000 (1,800-5,300) in 2005 (Fig. 3.7). The decline in bycatch was driven by a decline in fishing effort (Table 3.4) and an estimated decrease in population size.

Estimated population size matched observed population size with evidence of a decline in abundance during the study period (Fig. 3.8). The median estimated change in population size between 1987 and 2005 was -49% (-75% to -2%), with only a 2% probability that the population did not decline. There was 100% probability that the decrease in population size was greater during the first half of the study period 1987-1996 (average change of -4.2%, -8.0 to -0.7% per year) than the second half 1996-2005 (-3.1%, -7.0 to 0.5% per year). There was a 5% probability that the population did not decline between 1996 and 2005. The posterior for estimated population growth rate in the absence of bycatch differed strongly from the implicit prior (Fig. 3.9). The median estimated population growth rate in the absence of bycatch was 0.99 (0.95-1.03).

Scenarios 2 and 3

In Scenario 2, the density-independent model of a single population was fitted to the same data as in Scenario 1, except that only pregnancy data from healthy females were used. The observed pregnancy rate for healthy mature females, 0.59, was higher than for all mature females. The estimated birth rate in Scenario 2 was 0.84 (0.73-0.92) male and female calves per mature female; higher than the observed pregnancy rate and higher than the estimated birth rate in Scenario 1 (Fig. 3.10). Median estimated natural survival rates were lower in Scenario 2 (0.80, 0.82, 0.86, and 0.86)

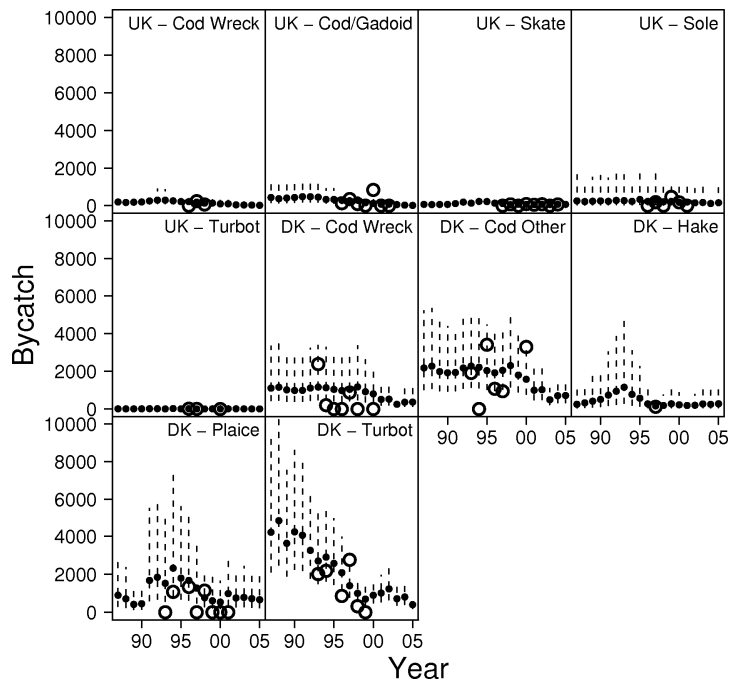


Figure 3.6. ‘Observed’ (open circles) and predicted (points and lines) bycatch of males and females in the ten fisheries for the density-independent model of a single population (Scenario 1, Table 3.6). Observed values represent bycatch calculated from the observed bycatch rate in a given year (actual observed bycatch divided by observed effort multiplied by total effort). Points and dashed lines represent the median and 95% interval of predicted values for bycatch (Eq. 3.23) from the posterior sample, respectively.

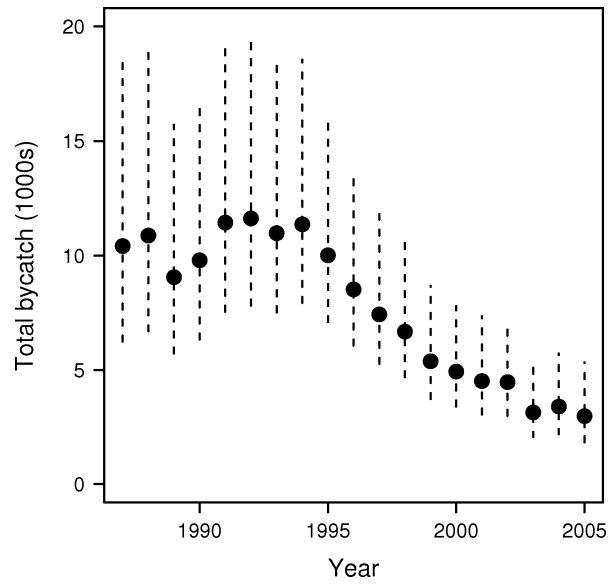


Figure 3.7. Predicted bycatch of males and females in all ten fisheries for the density-independent model of one population (Scenario 1, Table 3.6). Points and dashed lines represent the median and 95% interval of predicted values for bycatch (Eq. 3.23) from the posterior sample, respectively.

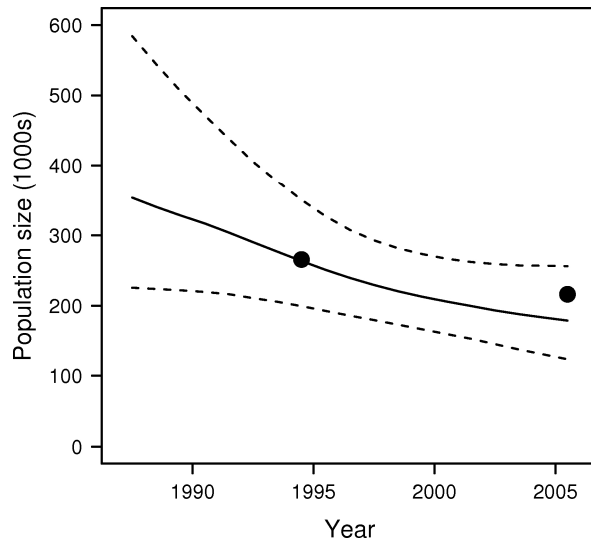


Figure 3.8. Observed (points) and predicted (lines) total number of males and females during the study period for the density-independent model of a single population (Scenario 1, Table 3.6). The solid line represents median values from the posterior sample and the dashed lines represent the 95% interval of values from the posterior sample.

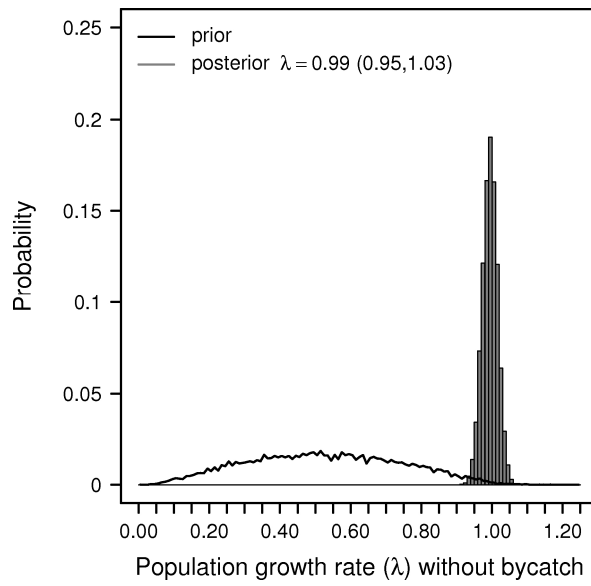


Figure 3.9. Prior and posterior probability distributions for population growth rate in the absence of bycatch for the density-independent model of a single population (Scenario 1, Table 3.6). The distributions for population growth rate were derived from the samples of maturity, birth and natural survival rates from the joint prior and joint posterior. The median posterior population growth rate was 0.99 with a 95% interval of 0.95-1.03.

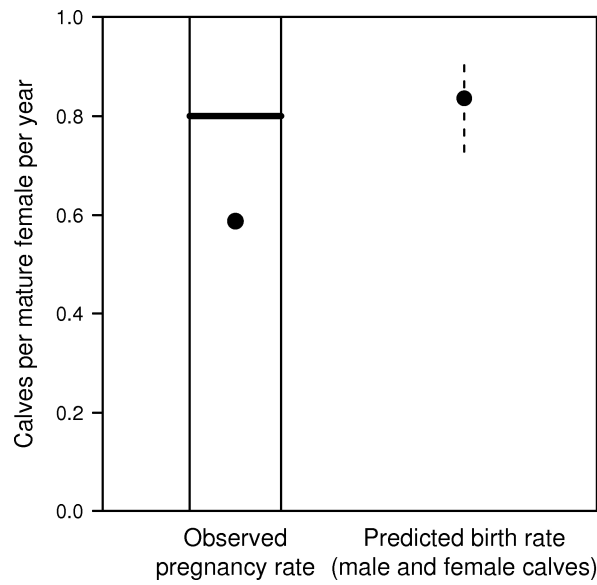


Figure 3.10. Observed pregnancy rate and predicted birth rate for the density-independent model of a single population with pregnancy data from only ‘healthy’ females (Scenario 2, Table 3.6). The boxplot on the left represents the distribution of observed pregnancy rates across years during the study period (point represents the overall pregnancy rate). The data point and dashed line on the right represent the median and 95% interval of predicted values for birth rate (male and female calves) from the posterior sample, respectively.

than in Scenario 1 (0.81, 0.83, 0.87, and 0.88) and resulted in a slightly better fit to the data on age structure of natural mortality (Fig. 3.11). The lower estimated survival rates, but higher estimated birth rate, resulted in an estimated population growth rate (1.00, 0.96-1.05) that was similar to but slightly higher than that in Scenario 1 in the absence of bycatch. The estimated change in population size during the study period under Scenario 2 was also slightly higher than that in Scenario 1 (-46%, -74 to 10% with a 4% probability of increase). Ignoring the pregnancy data altogether (Scenario 3) resulted in an estimated birth rate that was very near the upper limit of the prior 0.97 (0.87-1.00) and even lower survival rates (0.80, 0.81, 0.86, and 0.85). The estimated population growth rate in the absence of bycatch was 1.01 (0.96-1.06) under Scenario 3 and the estimated change in population size during the study period was -44% (-73% to 12%) with a 5% probability of increase.

Scenario 4

The model for Scenario 4 was identical to that for Scenario 1 except that calves of bycaught mothers, who were not bycaught themselves, were assumed to die as a result of abandonment (Eq. 3.10). The results for Scenario 4 were very similar to those for Scenario 1. The median estimated natural survival rate of calves was slightly higher, 0.82 (0.74-0.89), than under Scenario 1, but the median estimated natural survival rates for other ages did not change. Despite the small change in the natural survival rate of calves, the estimated population growth rate in the absence of bycatch in Scenario 4 was identical to that in Scenario 1.

Scenario 5

Under Scenario 5, bycatch rates in Danish fisheries during 2002-2005 were assumed to be half those in previous years. Thus, the main result of this Scenario was a decrease in estimated bycatch during 2002-2005. Bycatch estimates for these years were 55-57% of the corresponding estimates in Scenario 1. Bycatch estimates for years prior to 2002 were similar between Scenarios 1 and 5. The estimated bycatch in 2005 under Scenario 5 was 1700 (1000-3100). There was no difference in the estimated population growth rate in the absence of bycatch between Scenario 1 and Scenario 5, however the probability that the population increased between 2002 and 2005 rose from 9% to 16%.

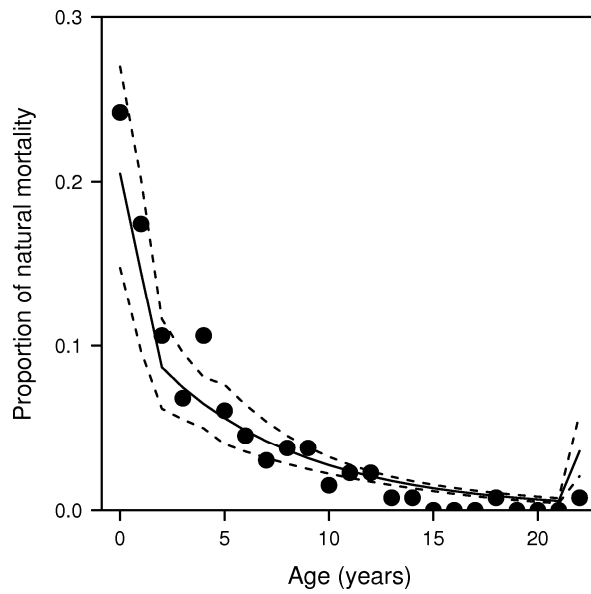


Figure 3.11. Observed (points) and predicted (lines) age structure of natural mortality for the density-independent model of a single population with pregnancy data from only ‘healthy’ females (Scenario 2, Table 3.6). Observed values represent overall proportions (data pooled across years) and predicted values represent average proportions across all years of the study period. Solid line indicates median values from posterior sample and dashed lines represent the 95% interval of values from the posterior sample. Note that the model was fitted to the data from individual years separately (Eq. 3.15), not the pooled data presented in this Figure.

Density-dependent model of single population

Scenario 6

Scenario 6 modelled a single population with density-dependent dynamics. The constraints on parameter space that were implemented for this model resulted in realized priors that were different from uniform distributions for several parameters (Fig. 3.12). The median estimated mean birth rate during the study period was 0.65 (0.58-0.73)—identical to the estimated birth rate in Scenario 1. However, the median estimated survival rates were higher under Scenario 6 (0.83, 0.84, 0.89 and 0.89). The estimated decline in population size during the study period was less under Scenario 6 than under Scenario 1: -31% (-53 to 21%) with a 9% probability of increase. The average rate of change during the latter half of the study period was -1.5% per year (-3.3 to 1.6%) with a 16% probability of increase between 1996 and 2005. Estimated population size was lower in 1987 and slightly higher in 2005 than in Scenario 1 (Fig. 3.13). These differences in population size resulted in slightly lower median estimates of bycatch in earlier years (e.g., 10,800 in 1992), and higher estimated bycatch in later years (3,600 in 2005) than in Scenario 1.

The posterior probability distribution for the number of female non-calves at carrying capacity was broad and relatively uniform over the part of the prior that was greater than the estimated initial number of female non-calves (150,000-500,000; Fig. 3.12). The median of the posterior for maximum birth rate was 0.70 male and female calves per mature female per year, but the interval of 95% probability, 0.60-0.91, was wide and ranged near the assumed maximum of 1. Median estimated maximum population growth rate was 1.02 (1-1.07), but its posterior distribution was similar to the realized prior (Fig. 3.14). Thus, the combination of data and model in Scenario 6 provided little information about density-dependence including carrying capacity, current population depletion (size relative to carrying capacity), and maximum population growth rate.

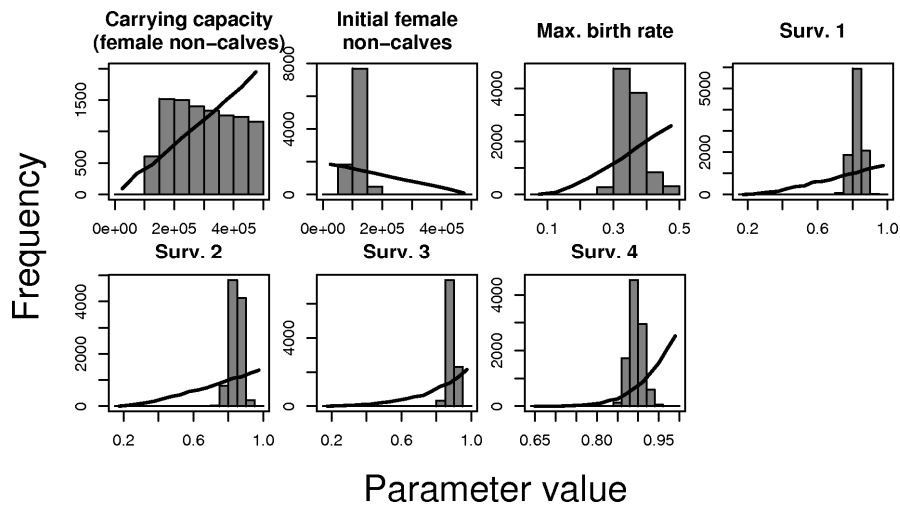


Figure 3.12. Marginal posterior probability distributions of selected estimated parameters (Table 3.5) of the density-dependent population model of a single population (Scenario 6, Table 3.6). Black lines and grey bars are histograms of samples of 10,000 parameter values from the joint prior and posterior, respectively.

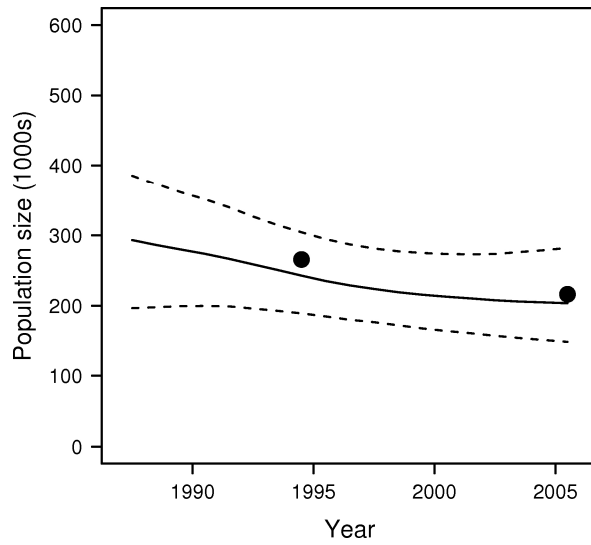


Figure 3.13. Observed (points) and predicted (lines) total number of males and females during the study period for the density-dependent model of a single population (Scenario 6, Table 3.6). The solid line represents median values from the posterior sample and the dashed lines represent the 95% interval of values from the posterior sample.

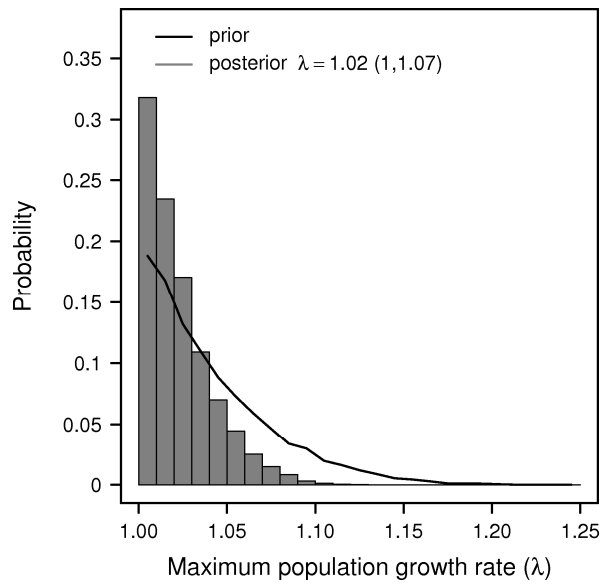


Figure 3.14. Prior and posterior probability distributions for maximum population growth rate in the absence of bycatch for the density-dependent model of a single population (Scenario 6, Table 3.6). The distributions for population growth rate were derived from the samples of maturity, birth and natural survival rates from the joint prior and joint posterior. The median posterior maximum population growth rate was 1.02 with a 95% interval of 1-1.07.

Density-independent model of two subpopulations

Scenario 7

Scenarios 7-9 modelled the harbour porpoise population in the study area as comprising two distinct subpopulations (Fig. 3.1) with density-independent dynamics. These models were fitted to the data on abundance, pregnancy, age at death and bycatch disaggregated by area. In Scenario 7 separate birth rates were estimated for the two subpopulations, but it was assumed that no animals dispersed between the subpopulations.

Estimated birth rates were very similar between the two subpopulations: 0.64 (0.52-0.76) male and female calves per mature female for the northern subpopulation and 0.65 (0.54-0.76) for the southern, even though observed pregnancy rates were different: 0.46 and 0.31 for the northern and southern subpopulations, respectively (Fig. 3.15). Because maturity and natural survival rates were assumed to be identical between the subpopulations, the similar birth rates resulted in nearly identical estimated population growth rates in the absence of bycatch (0.99, 0.96-1.03 and 1.00, 0.96-1.04).

Estimated total bycatch was higher in the first half of the study period for both subpopulations, but median bycatch was higher in the southern subpopulation (Fig. 3.16). Uncertainty in estimates of bycatch was greater in the two-subpopulation model than in the one-population model as indicated by the overdispersion parameter ($\theta=59$, 34-101 for Scenario 7 and $\theta=138$, 68-270 for Scenario 1; a smaller value equates to more overdispersion). The median estimated changes in the sizes of the two subpopulations during the study period were both negative (northern: -33%, -65 to 24%, southern: -55%, -76 to -17%), and neither matched the observed point estimates of abundance very well (Fig. 3.17). In particular, the estimated trend for the southern subpopulation failed to capture the observed increase in the point estimates of abundance.

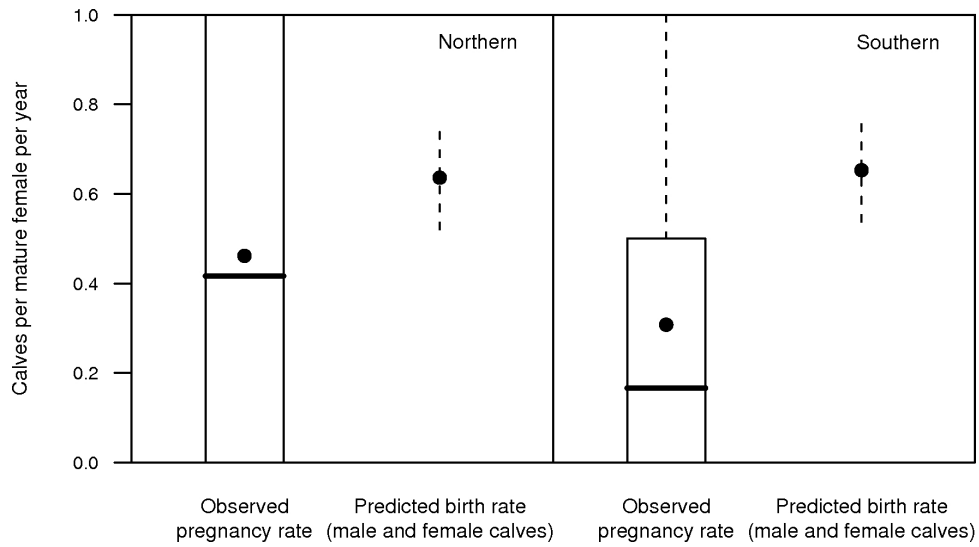


Figure 3.15. Observed pregnancy rate and predicted birth rate for the density-independent model of two subpopulations without dispersal (Scenario 7, Table 3.6). The left and right plots represent the northern and southern North Sea subpopulations, respectively. The boxplots represent the distribution of observed pregnancy rates across years during the study period (point represents the overall pregnancy rate). The data points and dashed lines on the right of each plot represent the median and 95% interval of predicted values for birth rate (male and female calves) from the posterior sample, respectively.

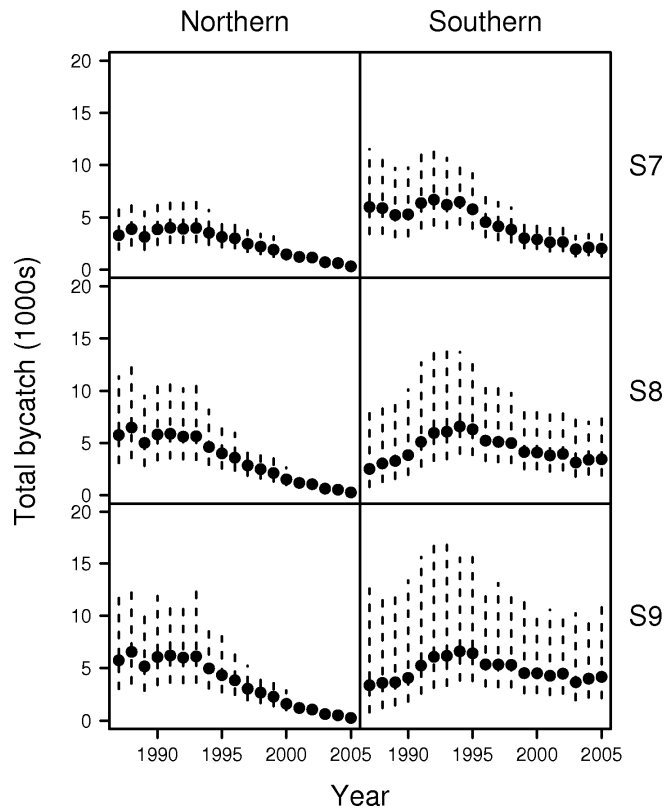


Figure 3.16. Predicted bycatch of males and females in all ten fisheries for the density-independent model of two subpopulations (Scenarios 7-9, Table 3.6). The left and right columns represent the northern and southern North Sea subpopulations, respectively. The three rows from top to bottom represent Scenarios 7-9, respectively. Points and dashed lines represent the median and 95% interval of predicted values for bycatch (Eq. 3.23) from the posterior sample, respectively.

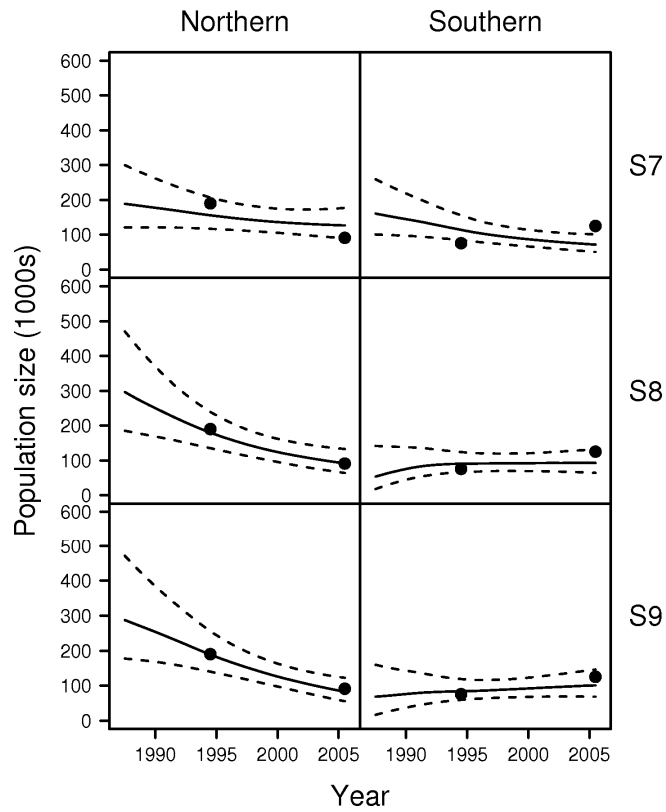


Figure 3.17. Observed (points) and predicted (lines) total number of males and females during the study period for the density-independent model of two subpopulations (Scenarios 7-9, Table 3.6). The left and right plots represent the northern and southern North Sea subpopulations, respectively. The three rows from top to bottom represent Scenarios 7-9, respectively. The solid lines represent median values from the posterior sample and the dashed lines represent the 95% interval of values from the posterior sample.

Scenario 8

In Scenario 8, birth rate was assumed to be identical for both subpopulations and animals were allowed to disperse from the northern subpopulation to the southern subpopulation at a constant, estimated rate. In this scenario, estimated changes in the sizes of the two subpopulations more closely matched the observed trends in the point estimates of abundance (Fig. 3.17). The estimated change in the northern subpopulation was -69% (-84 to -38%) with <1% probability of increase, while the estimated change in the southern subpopulation was 75% (-46 to 495%) with >80% probability of increase. An estimated annual dispersal rate of 0.04 (0.02-0.06) from the northern subpopulation to the southern subpopulation drove these different trends in abundance. Because the dispersal rate was assumed to be constant over time, the number of animals dispersing decreased as the northern subpopulation decreased, so the rate of increase in the southern subpopulation decreased during the study period (Fig. 3.17).

The different estimated population trends in Scenario 8 relative to Scenario 7 resulted in somewhat different trends in total bycatch (Fig. 3.16). The decrease in total bycatch from the northern subpopulation during the study period was more pronounced in Scenario 8 compared to Scenario 7 as a result of the more pronounced decrease in the size of that subpopulation. Conversely, the decrease in total bycatch from the southern subpopulation during the last half of the study period was less pronounced in Scenario 8 compared to Scenario 7 because of the relative stability in the size of that subpopulation during those years. Also in Scenario 8, bycatch from the southern subpopulation was lower early in the study period as a result of the estimated small size of that subpopulation at that time. The median estimated bycatch in the south was higher in 2005 than in 1987 in Scenario 8.

Scenario 9

The results for Scenario 9 were very similar to those for Scenario 8. The estimated dispersal rate from the northern subpopulation in the first year was 0.020 (0.001-0.051). The estimated increase in the dispersal rate over time was 0.0025 (0.0002-0.0060) per year or 0.046 (0.004-0.108) for the entire study period. This estimated increase in the rate of dispersal resulted in a more continuous increase in the median estimated size of the southern subpopulation during the study period compared to

Scenario 8 (Fig. 3.17). Estimated trends in total bycatch were similar between Scenarios 8 and 9, although the uncertainty in individual estimates was greater in the latter, possibly because of the additional dispersal parameter being estimated (Fig. 3.16).

Discussion

The integrated population dynamics model, in combination with the data, provided estimates of the bycatch, size and growth rate of the harbour porpoise population in the North Sea during 1987-2005 with appropriate estimates of uncertainty. The model and data were not informative about the maximum number of harbour porpoise that could be supported in the area (carrying capacity), nor the maximum rate at which this population could grow at low density. Different model scenarios produced slightly different estimates, but general conclusions were similar. The largest differences in conclusions arose in scenarios with two subpopulations and the presence or absence of movement between these subpopulations. The lack of fit of the model to the life history data highlighted potential inconsistencies among the different datasets.

Bycatch

Median estimates of bycatch of harbour porpoise in UK and Danish set-net fisheries in the North Sea were generally higher than previous point estimates, especially earlier in the study period (Commission of the European Communities 2002, Vinther and Larsen 2004). For example, the median estimated bycatch in all Danish fisheries in 1987 and 1988 was about 70% greater than the estimate presented by Vinther and Larsen (2004), but the proportional difference in annual estimates between the studies declined to 3% by 2002. There were at least three reasons for these differences. First, previous estimates for some Danish fisheries were based on bycatch rates stratified by season, whereas my model did not allow for seasonal differences in bycatch rate. When bycatch rate was higher in seasons with less effort (e.g., season 3 in the cod-wreck fishery), my model estimated higher bycatch than would a stratified calculation. Second, the likelihood that I used for bycatch along with the low proportions of effort observed generally resulted in positively skewed estimates of bycatch (Fig. 3.7) so that median estimates were higher than direct calculations. An extreme example of this effect would be a fishery with no observed bycatch whose calculated bycatch rate would be zero, but whose estimated median bycatch rate

would be greater than zero. Third, bycatch rates in my model were related to porpoise abundance, whereas in previous estimates they were not. Linking bycatch rate to porpoise abundance resulted in somewhat different estimated trends in bycatch over time with bycatch generally being relatively higher in earlier years than was the case with previous estimates. Bycatch tended to be higher in earlier years because the estimated population size was greater, and the bycatch per unit effort per porpoise abundance was assumed to be constant over time. It is impossible to say whether my estimates of bycatch or the previous estimates of bycatch are more accurate. However, the substantial differences in estimates resulting from different data stratifications, observation models and process models highlight the uncertainty involved in estimating bycatch from observer data with low sampling coverage.

The statistically fitted population model provided not only median estimates of bycatch, but also probability distributions for these estimates from which measures of uncertainty could be derived. Previous estimates of bycatch in Danish fisheries have been presented without quantitative measures of uncertainty (Vinther and Larsen 2004) or with CVs derived from bootstrapping of the observer programme data (Vinther 1999). The latter approach resulted in CVs ranging from 0.16-0.59 for mean estimated annual bycatch in individual fisheries and a CV of 0.12 for total bycatch. The posterior probability distributions in the base scenario of my study had CVs ranging from 0.19-1.31 with a mean CV of 0.62 for annual estimates of bycatch in individual fisheries and CVs ranging from 0.22-0.30 with a mean CV of 0.25 for estimates of total annual bycatch in UK and Danish fisheries. These CVs indicate substantial uncertainty that must be acknowledged when considering my estimates of bycatch.

Individual bycatch events are relatively rare and their occurrence in space and time can be highly clustered as a result of the spatiotemporal distribution of fisheries and animals (Vinther and Larsen 2004). Furthermore, observer coverage is usually not distributed randomly or evenly in space and time. Thus, simple statistical approaches to estimating uncertainty in estimates of bycatch rate are prone to underestimating uncertainty. There are multiple design- and model-based approaches that can be taken to estimate uncertainty in estimates of bycatch from observer programme data (e.g., Miller and Skalski 2006). The model-based approach that I used (beta-binomial

likelihood) provided estimates of uncertainty that were similar to or greater than previous estimates derived from bootstrapping. Thus, my approach provides an appropriate method for incorporating data on bycatch rate from observer programmes into integrated population dynamics models.

There are many potential biases in the observer programme data that further increase the uncertainty in my estimates of bycatch. Vinther and Larsen (2004) outline several potential biases in the observer programme data from Denmark, and many of these biases are also applicable to the UK data. Observer coverage of total fishing effort was generally very low (1% or less), which increases the probability that the observer data were not representative of all fishing effort simply as a result of chance. The Danish fishing effort that was observed was also biased toward larger vessels for cost and safety reasons. Vinther (1999) suggested that fishing practices are similar between large and small vessels in Danish fisheries, but small vessels tend to fish in more coastal areas. If smaller vessels had different bycatch rates or different numbers of landings or hauls per day at sea than larger vessels, my estimates of bycatch rate and total fishing effort, respectively, would be biased. It is difficult to say what those biases might be. In general, fishing effort within a defined fishery was assumed to be uniform and variability in fishing practices within a fishery could have created bias. For example, Vinther and Larsen (2004) point out that different types of net are used in the Danish plaice fishery and suggest that bycatch in the plaice fishery might be overestimated because of a higher bycatch rate with one of the net types. Fishing practices might also have changed over time within a fishery. For example, the use of acoustic alarms has been mandatory in the Danish cod-wreck fishery since 2000 and this might have reduced the bycatch rate during the last 4-5 years of my study period. As Scenario 4 demonstrated, a reduction in bycatch rate would bias my baseline estimates of bycatch upward. I assumed a constant rate of bycatch per unit effort per porpoise abundance, and this rate was estimated from observer programme data from earlier years (1993-2001). I also assumed that the amount of landings and number of hauls per day at sea were constant over time in Danish and UK fisheries, respectively. If these ratios have changed over time my estimates of total fishing effort would be biased. For example, there was a decrease in fishing trip length and a corresponding increase in the proportion of a trip spent steaming to the fishing ground in the Danish cod fishery between 1987 and 2001 (Vinther and Larsen 2004). Assuming the same

landings per day fishing, the landings per day at sea would have been lower in more recent years relative to earlier years. By assuming constant landings per day at sea, bycatch has been overestimated in recent years relative to earlier years (Vinther and Larsen 2004). A last potential bias in the observer programme data is the dropout of porpoise from fishing nets at or below the surface when nets are being brought out of the water. It is possible that some porpoise became entangled and drowned but fell out of the nets before the observers were able to see them. Dropout would bias estimates of bycatch downward.

The most certain and probably the most influential bias in my estimates of bycatch was an underestimation as a result of the exclusion of unobserved fisheries, fisheries in which no bycatch was observed, and fisheries of other countries. There are several fisheries of the UK (dogfish, monkfish and herring) and Denmark (sole) that had observer effort during my study period but had no observed bycatch of harbour porpoise. For fisheries in which bycatch has not been documented it is almost a philosophical decision whether these fisheries should be included in the model or not. The absence of bycatch in an observed sample of fishing effort does not preclude bycatch occurring in the unobserved effort, but there is no way to determine whether bycatch could occur. If one assumes that bycatch is possible in these fisheries sampling theory can provide probability distributions for the occurrence of events even without non-zero observations. However, I found that the low proportions of effort sampled resulted in distributions that were too unconstrained to be informative. Following Vinther and Larsen (2004) I excluded fisheries without observed bycatch from my analysis and effectively assumed that no bycatch occurred in these fisheries. If bycatch did occur in these fisheries, my estimates of bycatch would be underestimates.

Bycatch of harbour porpoise has been documented in North Sea fisheries of countries other than the UK and Denmark including Germany, the Netherlands and Norway (Benke 1994, Bjørge and Øien 1995, Kock and Flores 2003, Leopold and Camphuysen 2006). The bycatch rate per unit fishing effort in these fisheries might be similar to that in the fisheries that I considered (Kock and Flores 2003). However, further data on bycatch rate and total fishing effort are required before these fisheries can be incorporated in an analysis like that presented here. In the meantime, my

estimates of bycatch are almost certainly biased downward to some extent because of the exclusion of these fisheries.

One-year-old females were estimated to be the most vulnerable to bycatch (Fig. 3.2), which could indicate differences in their behaviour (e.g., inexperience) or differences in their spatiotemporal distribution in relation to fishing operations. One-year-olds were the most common age class in the sample of directly bycaught females from Denmark and the UK sample of stranded females that were diagnosed as having died from bycatch (Table 3.1, Fig. 3.5). Other studies have found similar age structures for samples of bycaught harbour porpoise. For example, Read and Hohn (1995) found that 1 and 2 years were the modal ages for male and female harbour porpoise that were incidentally caught in gillnets in the Gulf of Maine. The most frequent age class of bycaught harbour porpoise in Swedish fisheries in the Skagerrak and Kattegat Seas was 1 year (Berggren 1994). In contrast, calves were more common than other ages in the sample of directly bycaught females from the UK. Calves were also the most frequent age class in a sample of directly bycaught porpoise from Iceland and a larger sample of bycaught animals from Danish waters that included the animals used in my study, but also included animals from areas and years that were not covered by my study (Lockyer and Kinze 2003, Ólafsdóttir et al. 2003).

There are several potential biases in the age structure data that I used for bycatch mortality. First, carcasses of different sizes might strand with different probabilities if they decompose at different rates, drift differently in the water or sink at different rates. The higher frequency of 1-year-olds than calves in the sample of stranded bycaught animals from the UK could have arisen if the carcasses of calves were less likely to strand. However, this pattern was not evident in the sample of stranded animals that were diagnosed as having died from natural causes. Different sizes of animals might also drop out of fishing nets with different probabilities. The higher frequency of 1-year-olds than calves in the sample of directly bycaught animals from Denmark could have arisen if calves were more likely to drop out of nets before being sampled. Given these potential biases and the different age structures observed in the different sub-samples of bycaught porpoise, it is not possible to definitively say whether 1-year-old animals were more vulnerable to bycatch than other ages.

Population growth rate and life history

My model suggested that there is a very high probability that bycatch between 1987 and 2005 resulted in a decrease in the number of harbour porpoise in the North Sea, with a greater rate of decline earlier in the study period. Thus, my results suggest that there is a high probability that the harbour porpoise population in the North Sea could not sustain bycatch of the magnitude experienced during the 1990s. That being said, there were substantial probabilities that the population did not decline, especially during the latter half of the study period (5% in the base Scenario 1 and 16% in the density-dependent Scenario 6). It is possible that the population could sustain the lower estimated bycatches near the end of the study period.

While overall changes in population size are of conservation interest, the rate at which a population can grow in the absence of anthropogenic removals is of biological interest. When I assumed that population growth was density-independent (Scenarios 1-5), the estimated population growth rate in the absence of bycatch was surprisingly low: around 0 with 95% probability intervals ranging from a 5% decrease to a 6% increase per year. It is not surprising then that the estimated bycatch produced a decline in the population. When population growth was assumed to be density-dependent (Scenario 6), the estimated maximum population growth rate at low density was similarly low: 2% per year with a 95% probability interval of 0-7%, although the posterior for maximum population growth rate was very similar to the assumed prior.

It appeared that the main reason for the low estimated population growth rate in the absence of bycatch was the life history data that the model was fitted to. Fifty percent of females were estimated to be sexually mature by 4-5 years of age and 90% by about 6 years of age. However, few animals >10 years of age were observed in the samples of bycaught and stranded specimens from the UK and Denmark (Table 3.1). Together the age structure and sexual maturity data imply a short potential reproductive lifespan for females. Given that the gestation period for harbour porpoise in the North Sea is 10-11 months (Sørensen and Kinze 1994, Learmonth 2006), females would have to give birth almost annually for substantial population growth. In contrast, the observed pregnancy rate was only about 60% for 'healthy' females. Even with slightly higher than observed survival and birth rates, the model suggested a limited scope for population growth.

The life history of the harbour porpoise has been characterized as a fast one in the western North Atlantic, with sexual maturity at 3-4 years of age, a short lifespan (animals older than 12 years were uncommon) and near-annual reproduction by mature females (Read 1990a, Read and Hohn 1995). Similar ages at sexual maturity and age structures have been observed in the eastern North Atlantic (Clausen and Andersen 1988, Sørensen and Kinze 1994, Lockyer 1995b, Lockyer et al. 2001, Lockyer and Kinze 2003, Ólafsdóttir et al. 2003). The observed age structure of natural mortality in my study was similar, but the estimated age at which 50% of females were sexually mature (4-5 years) was at the higher end of the range of mean ages at sexual maturity from previous studies. There are numerous techniques for estimating age at sexual maturity and estimates from different techniques can differ by two years or more depending on the resolution of ages, the assumed maturity ogive and the implicit weighting of samples of different ages (DeMaster 1984, Ólafsdóttir et al. 2003). My method was essentially a logistic regression with all animals assumed to be at the mid-point of their estimated age class (e.g., a 4-year-old was assumed to be exactly 4.5 years old). Thus, my method would produce a higher age at sexual maturity than methods that simply use integer ages. In all studies the range of ages at which female harbour porpoise matured sexually was several years with immature animals as old as 5 or 6 years (Van Utrecht 1978, Ólafsdóttir et al. 2003).

Pregnancy rates of harbour porpoise are quite variable among studies. Some studies have documented pregnancy rates >90% implying annual reproduction for most mature females (Read and Hohn 1995, Ólafsdóttir et al. 2003) while other studies have found lower pregnancy rates from 86% to as low as 42% (Read 1990a, Sørensen and Kinze 1994, Learmonth 2006). Some of the variability in these pregnancy rates arose because of the timing of samples. For instance, one might expect higher pregnancy rates earlier in gestation. Pregnancy rates also differed depending on whether samples from the calving and breeding season (June-August) were included (Read 1990a). The criteria used to establish pregnancy created further variability. Estimates based on the presence of a corpus luteum often differed from estimates based on the presence of a foetus (Learmonth 2006). In this study I excluded samples from June-August when estimating birth rate and I used the presence of a foetus to

establish pregnancy. The observed pregnancy rate for all mature females was 41%, but this increased to 59% when only healthy females were considered.

My fitted model estimated a birth rate that was higher than the observed pregnancy rate. The estimated age structure of natural mortality was also a poor fit to the data. Specifically, the model estimated higher survival rates than were consistent with the data. The cause of these inconsistencies between the model predictions and the life history data can be understood by considering the population growth rate. The observed age structure of animals that died naturally implied a relatively low survival rate and short lifespan. However, that same age structure, with many more juveniles than older animals also implied a relatively stable or growing population. The observed low pregnancy rate, when combined with the apparently low survival rates, suggested a declining population whose mortality age structure would have been more even. Thus, the life history estimated by the model was a compromise with a higher than observed birth rate and a more even than observed age structure of natural mortality. This conclusion is supported by the results of Scenarios 2 and 3: when the observed pregnancy rate increased or was ignored, the birth rate was estimated to be even higher and the model fitted the natural mortality data better.

Population models enforce mathematical consistency among birth and survival rates, population growth rate, and age structure. Thus, population models are useful for highlighting apparent inconsistencies between datasets and potentially reconciling these datasets (Punt et al. 2006, Hulson et al. 2008). My model was not able to reconcile the low observed pregnancy rate with the age structure of natural mortality. The estimated life history in my model was a compromise between the data on pregnancy rate and the data on age structure of natural mortality. The resulting probability distribution for each parameter (e.g., birth rate) was unimodal. Another way to represent the uncertainty arising from the inconsistency between datasets might have been to allow for multi-modal posterior probability distributions representing estimates based on different datasets (Schnute and Hilborn 1993).

The fitting of my integrated population dynamics model to multiple datasets (pregnancy rate, age structure of mortality, abundance) allowed me to estimate birth and survival rates (and therefore population growth rate) simultaneously. It is obviously impossible to estimate survival rates from data on reproductive rate alone,

but data on age structure can theoretically be used to estimate survival rates and population growth rate simultaneously. The latter estimation is difficult because the correlation between survival and population growth can result in quite similar age structures for different combinations of the two. The addition of data on reproductive rate can enforce consistency among reproductive, survival and population growth rates, but it does not eliminate the difficulty in estimation caused by the correlation between survival and population growth rates. Thus, estimates of survival rates from age structure data have typically relied on assumptions about population growth rate (Caughley 1966, Stolen and Barlow 2003). Udevitz and Ballachey (1998) suggest that data on standing age structure and data on age structure of mortality allow one to estimate survival rates and population growth rate simultaneously. At least two studies have estimated harbour porpoise survival rates and population growth rates from age structure data alone. Berggren and Wade (2003) estimated the rate of population growth for harbour porpoise in Swedish waters while Moore and Read (2007) estimated population growth rate for harbour porpoise in the Gulf of Maine/Bay of Fundy. Both studies relied on age-at-death data from stranded and bycaught animals although Moore and Read (2007) also incorporated information on birth rate through an informative prior. The additional data that my model was fitted to (e.g., abundance, bycatch rate) provided more, independent information about population growth rate and allowed the estimation of population size and bycatch.

My estimates of the density-independent population growth rate for harbour porpoise in the North Sea suggest that even in the absence of bycatch, there were almost equal probabilities that the population would have decreased or increased during the study period. Berggren and Wade (2003) also found a substantial probability of population decline in the absence of bycatch for harbour porpoise in Swedish waters. There are several possible reasons why the harbour porpoise population in the North Sea might have remained stable or even declined in the absence of bycatch. It is possible that density-independent factors were acting to reduce survival or reproductive rates. For example, polychlorinated biphenyl pollutants increase the susceptibility of harbour porpoise to infectious disease (Hall et al. 2006). In a density dependence context it is possible that population growth was prey-limited and that the population was at or near the carrying capacity of the environment. Furthermore, a decline in carrying capacity could have caused a decline in population size. Unfortunately my

combination of model and data did not shed any light on what that carrying capacity was.

My model was not informative about what the maximum population growth rate was at low density (intrinsic rate of increase; Caughley and Birch 1971), but there was a high probability that it was <10% per year. Moore and Read (2007) estimated population growth rate in the absence of bycatch, but restricted it to be positive. Their 90% probability interval was 0-11% per year. Previous estimates of harbour porpoise population growth rates based on survivorship curves for other mammals also suggest that the maximum is likely $\leq 10\%$ (Barlow and Boveng 1991, Woodley and Read 1991, Caswell et al. 1998). An international working group suggested that the harbour porpoise might be relatively more *r*-selected than other cetacean species, but recommended 4% as a conservative estimate of the maximum rate at which harbour porpoise populations could grow (IWC 2000). Certainly some features of harbour porpoise life history like body size, age at maturity and life expectancy are more *r*-selected relative to other cetaceans (Stearns 1976, Millar and Zammuto 1983). Regardless, my results are consistent with those of previous studies that suggest the scope for growth in harbour porpoise populations is relatively limited.

As noted earlier, bycatch was likely underestimated in my model because of the exclusion of unobserved fisheries and fisheries of countries other than the UK and Denmark. It is difficult to predict how higher estimates of bycatch might have affected the model predictions, but it is possible that the estimated population growth rate in the absence of bycatch would have been higher to compensate for the additional mortality and thus maintain a similar estimated trend in population size. Alternatively, the constraints imposed by the life history data might have resulted in a similar estimated population growth rate in the absence of bycatch and a more negative trend in population size during the study period. I suspect that the constraints imposed by the life history data would have prevented a substantial increase in the estimated population growth rate, but of course this would depend partially on the magnitude of the extra bycatch.

Carrying capacity

My analysis provided essentially no information on carrying capacity and thus provided no information about the current status of the harbour porpoise population in

the North Sea relative to its carrying capacity. My study period was 18 years and I had only two, similar abundance estimates during that time. A longer time series of abundance estimates with greater contrast in population size might have provided more information about the nature of density dependence including carrying capacity and maximum population growth rate (Goodman 1988, Brook and Bradshaw 2006). Another approach to estimating carrying capacity and current depletion would have been to derive a complete historical time-series of fishing effort and assume that the population was at carrying capacity at the start of this time-series. However, data on fishing effort, with the level of detail used in this study, are not available for years prior to the mid-1980s. Furthermore, this approach would require major assumptions about historical bycatch per unit fishing effort per porpoise abundance. A simpler stock reduction analysis would probably be a better place to start reducing uncertainty in what the population size might have been prior to bycatch (Walters et al. 2006). Changes in carrying capacity over time further complicate any analysis of density dependence. I did not consider any scenarios where carrying capacity changed over time because of the poor results of the scenario with constant carrying capacity.

Population structure

Population structure is an important consideration when modelling population dynamics. Several studies have found genetic differentiation between harbour porpoises in different parts of the North Sea including north-south differences and east-west differences (Walton 1997, Tolley et al. 1999, Andersen et al. 2001). Recent studies suggest that the pattern of genetic differentiation in harbour porpoises of the Northeast Atlantic might be best described as isolation-by-distance (Tolley and Rosel 2006, Fontaine et al. 2007a). Lahaye et al. (2007) found different concentrations of trace elements in harbour porpoises from different parts of the North Sea and suggested that these differences might reflect long-term segregation of animals between these areas. The aforementioned evidence indicates that there might be genetic and ecological differences among harbour porpoises within my study area. However, from the available information it is not possible to determine whether distinct subpopulations exist or if they do where the boundaries between these subpopulations might be. I explored one simple hypothesis regarding population structure within the North Sea: northern and southern subpopulations. If an isolation-by-distance pattern applies at the spatial scale of my study area, then distinct

subpopulations would not be a realistic representation of population structure within the area. In that case, the designation of subpopulations would simply be a convenient way of delineating the mostly continuous distribution of harbour porpoise across the area.

The point estimates of abundance for the northern and southern subpopulations suggest opposite changes in population size between 1994 and 2005 in July (SCANS-II 2008). Population dynamics models are useful for exploring hypotheses and reconciling trend data in the context of population structure (Punt et al. 2006). My model suggested that the different trends in the north and south were likely not a result of different rates of population growth within subpopulations. Specifically, the constraints imposed by the life history data on population growth rate precluded a good fit to the increasing estimates of abundance for the southern subpopulation in the face of the estimated bycatch. The life history data were also not consistent with the decreasing estimates of abundance for the northern subpopulation. Model scenarios that allowed for dispersal of animals from the north to the south resulted in better fits to the abundance estimates, especially when the dispersal rate was allowed to increase throughout the study period. These model scenarios were intended to represent simple and distinct hypotheses regarding the growth rates of the subpopulations and rates of movement between the subpopulations. The scenarios were not necessarily realistic. For example, there could have been differential population growth and movement. Furthermore, the rate of movement between subpopulations would not likely be constant or change linearly. Nevertheless, my model scenarios suggested that dispersal or redistribution of harbour porpoise from the north to the south is a more plausible explanation for observed changes in abundance than different population growth rates within areas.

In the future, other data could be incorporated in integrated population dynamics models to better represent and estimate population structure and movement. For example, Bayesian analyses of genetic data provide posterior probability distributions for the number of subpopulations and for the geographic distribution of those subpopulations (Thatcher 2005, Fontaine et al. 2007a). These probability distributions could be incorporated in a population model as priors or a population dynamics model could be fitted to the genetic and other data simultaneously. That being said, the

representation of continuous population structures (e.g., isolation by distance) may be much more demanding computationally. A population dynamics model could also be fitted to genetic, telemetry and mark-recapture data to directly estimate movement rates of animals. Such data would help deal with the confounding between the estimation of growth rates for subpopulations and movement between those subpopulations.

Future directions

My integrated population dynamics model provided probability distributions for the bycatch, size and growth rate of the harbour porpoise population in the North Sea during 1987-2005 under several scenarios. These probability distributions allow for straightforward incorporation of estimation uncertainty into prediction for risk assessment, population viability analysis and management strategy evaluation using the population model (Harwood 2000, Maunder et al. 2000, Wade 2002a). For example, Chapter 4 describes management procedures that I developed to calculate bycatch limits for harbour porpoise in the North Sea and European Atlantic that will achieve specific conservation objectives. The integrated population dynamics model provided estimates of bycatch and population size for input to these procedures, and it was used to condition simulations designed to test the performance of those procedures.

One of the most useful outcomes of my modelling exercise, indeed any modelling exercise, is the generation of hypotheses that can be further tested with more data in the future. My model highlighted an apparent inconsistency between the data on pregnancy rate and the age structure of natural mortality. More data are needed on these aspects of the life history of harbour porpoise in the North Sea in order to resolve this conundrum. My model suggested that dispersal was a more plausible hypothesis than differential population growth for the observed changes in abundance in the northern and southern North Sea. Further data from genetic and telemetry studies could provide estimates of dispersal rates that could be used to evaluate this hypothesis. Abundance data were crucial for the analysis presented here; future estimates of abundance would be invaluable. Time-series of relative abundance, such as those derived in Chapter 2, could also be incorporated in the modelling framework. In general, integrated population dynamics models can accommodate an unlimited

range of hypotheses and data, and further research on harbour porpoise in the North Sea will help to refine the assessment presented here.

Chapter 4: Management procedures for calculating bycatch limits for harbour porpoise in the North Sea

Introduction

Ideally the bycatch of harbour porpoise in North Sea fisheries would be eliminated through technological modifications to fishing gear (Trippel et al. 2003, Larsen et al. 2007), acoustic alarms (Kraus et al. 1997, Trippel et al. 1999, Gearin et al. 2000) or the exclusion of fishing from areas used by harbour porpoise (Murray et al. 2000). Unfortunately, none of these approaches is currently feasible for stopping bycatch altogether. Given that bycatch of harbour porpoise will continue to occur in many fisheries in the foreseeable future, it is important to understand the maximum level of bycatch that these populations can sustain while still maintaining desirable conservation status. Management actions can then focus on ensuring that bycatch is kept below this level.

A common approach to calculating removal limits for a biological population is the stock assessment approach (Butterworth 2007). Under this approach, a population dynamics model is used to integrate available data and provide a best assessment of key biological parameters (e.g., population size and growth rate). Removal limits are then calculated based on some function of these biological parameters or based on simulations of the effects of different removals on the population in the near future. Estimates of biological parameters generally have associated measures of uncertainty that allow a more precautionary approach to setting removal limits. The stock assessment approach has often been applied to populations of marine mammals and other marine megafauna to manage anthropogenic removals including harvest (Witting and Born 2005) and bycatch (Burkhart and Slooten 2003, Lewison and Crowder 2003, Hoyle and Maunder 2004, Kaplan 2005, Zador et al. 2008). Despite the conservative elements inherent to modern stock assessment, it is still subject to failures arising from incorrect assessments (e.g., incorrect model specification and biased or misleading data) and there is no guarantee that the method for setting removal limits will perform desirably with respect to management and conservation objectives in the long-term (Butterworth 2007).

A preferable approach to managing removals from a population is to develop a robust, fully-tested management procedure that can be used to set removal limits. A management procedure can be defined as a procedure that takes information about a population as input and calculates a limit to removals that will achieve the desired management and conservation objectives (Rademeyer et al. 2007). Computer simulation can be used to explicitly evaluate the long-term performance of the management procedure. This simulation-testing technique is known as management strategy evaluation (MSE) in fisheries science and management (Kell et al. 2007, Rademeyer et al. 2007) and similar approaches have been used for other taxa (e.g., Milner-Gulland et al. 2001, Stephens et al. 2002, Bradshaw et al. 2006). Through simulation one can examine the performance of alternative management procedures under any scenario imaginable. Simulations should at a minimum address past data, future availability of data, dynamics of the population, dynamics of the removal process, and the environment (Rademeyer et al. 2007). Simulations can also be conditioned on the results of assessments, essentially a hybrid of the stock assessment approach and MSE.

Desirable features of any management procedure include a feedback mechanism by which new information about the population is incorporated over time, input data and parameters that are easily estimated and explicit accounting for uncertainty (Taylor et al. 2000). Management procedures can be classified as empirical or model-based (Rademeyer et al. 2007). Empirical management procedures set removals based directly on new data while model-based management procedures use new data to update estimates of the parameters of a model which are then used to set removals. Empirical management procedures are easier to understand and faster to implement, but tend to lead to more variability in removals over time than model-based management procedures. Model-based management procedures are more complex, but can learn about the dynamics of the population over time (closed-loop policies; Walters and Hilborn 1978). Thus, model-based management procedures have the potential to correct initial systematic errors in estimates of biological parameters (e.g., equilibrium population size, maximum population growth rate) and adjust the removal limit appropriately. Commonly, model-based management procedures are passive-adaptive whereby the learning process is dictated by natural variability and random errors (Walters and Hilborn 1978). Stock assessment is a model-based management

procedure and its long-term performance can be evaluated through MSE (Kell et al. 2005a, Schnute and Haigh 2006, Pastoors et al. 2007).

During the last 20 years or so, the MSE approach has become popular for managing removals from marine mammal populations. The International Whaling Commission (IWC) pioneered the use of MSE to evaluate the performance of management procedures for harvesting whales (de la Mare 1986). Using the MSE approach the IWC confirmed the shortcomings of its previous management procedure (the New Management Procedure) and developed more sophisticated management procedures that were robust to uncertainty and whose long-term performance with respect to management objectives was evaluated explicitly (Punt and Donovan 2007).

Aboriginal Whaling Management Procedures have been developed by the IWC to set strike limits for aboriginal subsistence harvests (IWC 2007a), and the Revised Management Procedure (RMP) was developed to set catch limits for commercial whaling (Hammond and Donovan In press). At the core of the RMP is the Catch Limit Algorithm (CLA), which is the mechanism that calculates catch limits based on time-series of historical catches and estimates of population size (Cooke 1999). The CLA is a model-based management procedure with primarily passive-adaptive behaviour. The specific CLA used was selected from a set of competing CLAs based on its performance with respect to catch-related and risk-related objectives (Punt and Donovan 2007).

The USA Government has also recognised the value of MSE and has developed the Potential Biological Removal (PBR) management procedure for managing all anthropogenic removals from marine mammal populations (Wade 1998, Taylor et al. 2000). The PBR procedure calculates removal limits from a single, current estimate of abundance and is therefore an empirical management procedure. New estimates of abundance allow for updated bycatch limits, but the PBR procedure has no inherent ability to learn. The PBR procedure was developed based on its performance with respect to risk-related criteria, specifically to maintain populations at an optimum sustainable population size which is defined as a population size above a population's maximum net productivity level (Gerrodette and DeMaster 1990). Since its development, the PBR procedure has also been used to calculate conservative removal limits for marine mammal populations in countries other than the USA (e.g., Johnston

et al. 2000, Berggren et al. 2002, Williams et al. 2008). In New Zealand, an adaptation of the PBR procedure has been used to manage bycatch of sea lions in a squid fishery. Extensive MSE simulations have been conducted, including conditioned simulations, to evaluate the management procedure's performance with respect to risk-related criteria for the sea lion population and catch-related criteria for the fishery (Maunder et al. 2000, Breen et al. 2003).

In 2000, a joint IWC/ASCOBANS (Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas) working group on harbour porpoise recommended the development of a management procedure that could be used to determine limits to bycatch that would achieve conservation objectives in the long term (IWC 2000). This working group further recommended that computer-based simulation models be used to test the performance of the management procedure to ensure that it is robust to a wide range of uncertainties with respect to the biology of harbour porpoise (e.g. stock structure), the estimation of population size and bycatch, and environmental variability.

The goal of this chapter was to develop a robust management procedure to generate bycatch limits for harbour porpoise in the North Sea based on available information. Following the recommendations of the IWC/ASCOBANS working group I used a MSE approach. I considered the PBR and CLA management procedures as candidates for my purpose. My specific objectives were: 1) compare and contrast the behaviour of the two procedures, 2) tune the procedures so that I would expect to achieve specific conservation objectives in practice, 3) conduct a set of generic simulation trials to evaluate the robustness of my tunings to a range of biases, stochasticity and uncertainty, 4) conduct conditioned simulation trials of the procedures for harbour porpoise in the North Sea using the results of the integrated population dynamics model (Chapter 3), and 5) calculate bycatch limits for harbour porpoise in the North Sea using the tuned procedures.

Methods

Conservation objectives

The first step in generating appropriate bycatch limits for harbour porpoise is the establishment of conservation and management objective(s) in quantitative terms.

These are management decisions. Conservation and management objectives related to bycatch generally fall into two categories: risk-related (e.g., minimise probability of population size declining to some threshold) and fishery-related (e.g., maximise catch, minimise variability in catch over time). There are implicit trade-offs between risk-related objectives and the socio-economic benefits derived from the fisheries. My goal was to develop a management procedure that would achieve specific conservation objectives, but I also evaluated the performance of the candidate management procedures with respect to fishery-related criteria.

European policymakers have not established specific conservation objectives for small cetaceans. Therefore, for the purposes of my work I adopted the interim conservation objective agreed by ASCOBANS (1997): to allow populations to recover to and/or maintain 80% of carrying capacity in the long term. Carrying capacity was defined as the population size that would theoretically be reached by a population in the absence of bycatch. Note that I did not need to know what this carrying capacity actually was to develop management procedures to set bycatch limits.

The ASCOBANS interim conservation objective was partially quantitative but two factors were not fully defined.

First, “long term” was not specified. I adopted a period of 200 years for the development of the management procedures. This long period was chosen to allow sufficient time for heavily depleted populations to recover even in the absence of bycatch if natural rates of increase were low. However, because the status of populations in the shorter term is also of interest for conservation, I examined delays in the recovery of depleted populations resulting from continued bycatch under the management procedures.

Second, the most obvious quantitative interpretation of “recovering to and/or maintaining 80% of carrying capacity” is that this is an expected target that should be reached on average (i.e., *at* 80% of carrying capacity). This is important because, as described below, the management procedures developed must be tuned to achieve the conservation objective. My first tuning therefore ensured that the procedures reached or exceeded the conservation objective target 50% of the time.

Alternatively, one could interpret the ASCOBANS interim conservation objective as meaning that the population should recover to and/or be maintained *at or above* 80% of carrying capacity. This could be implemented as a requirement to reach the target level a higher than average percentage of the time, although this percentage is not specified. To capture this alternative interpretation, I also tuned the management procedures to achieve the conservation objective 95% of the time. This is a much stricter target and this tuning produced more conservative procedures.

In addition, although the approach used to develop the management procedures explicitly takes account of uncertainty in our knowledge, the limits to this uncertainty cannot be explicitly defined by the conservation objective and must be determined by expert judgement of the plausibility of the extent of our uncertainty. I developed management procedures that were tuned to meet the conservation objective assuming a certain baseline level of uncertainty (e.g., conservative values for maximum population growth rate and the population level that results in maximum productivity) and then tested the robustness of the procedures to additional sources of uncertainty, following the approach used in the development of the CLA and PBR procedures. An extreme alternative is to tune the procedures to meet the conservation objective in the face of a worst-case scenario. By definition, this scenario has lower plausibility than the baseline scenario, but for comparison I also present results for this much more conservative approach.

It is critically important to note that although the management procedures presented here are generic, the specific results presented are entirely dependent on the conservation objective adopted. If it is determined that alternative and/or additional conservation/management objectives are appropriate, the management procedures can easily be tuned to the new objective(s) when a final policy/management decision is taken.

Management procedures

Full specifications of the PBR and CLA management procedures are described below. In brief, both procedures take information about a population as input and then output a bycatch limit. The PBR procedure is an empirical management procedure that takes a single, current, 'minimum' estimate of absolute population size as input. The CLA procedure is a model-based management procedure that takes time-series of estimates

of absolute population size and estimates of absolute bycatch as input. Both procedures explicitly incorporate uncertainty in the estimates of population size. Thus, the procedures also require estimates of the precision of the estimates of population size as input. Under the PBR procedure, the calculation of the bycatch limit proceeds using a single, relatively simple equation. Under the CLA procedure, the calculation of the bycatch limit is slightly more demanding computationally. The CLA procedure involves statistically fitting a simple population model to the input data series and then calculating the bycatch limit as a function of several quantities estimated through the model fitting.

A key element of both procedures is the ability to tune the procedure, or adjust the bycatch limits, so that specific conservation/management objectives are achieved. The PBR procedure incorporates one tuning parameter, while the CLA procedure has three tuning parameters. Another important element of both procedures is that new data on the population can be used to update the bycatch limit. However, only the CLA procedure makes use of historical data on the population. This feature of the CLA procedure allows a more sophisticated rule for setting the bycatch limit whereby a threshold population size relative to carrying capacity can be specified below which the bycatch limit is set to zero. Under the PBR procedure, the bycatch limit is approximately a constant proportion of the estimated population size.

The management procedures are designed to be applied at the spatial resolution of defined management areas. The procedure is applied separately to each management area resulting in a separate bycatch limit for each area.

PBR

Under the PBR management procedure the bycatch limit for a management area is calculated using a relatively simple equation and a current estimate of absolute abundance (Wade 1998):

$$[4.1] \quad CL_{j,t} = N_{j,t}^{\min} \frac{1}{2} R^{\max} F$$

where $CL_{j,t}$ is the bycatch limit for area j in the year following time t , $N_{j,t}^{\min}$ is the ‘minimum’ estimated number of animals in area j at time t , R^{\max} is maximum

population growth rate (i.e., population growth rate at low density), and F is a recovery factor—a parameter that can be tuned so that the PBR procedure achieves specific management objectives. Errors in estimates of abundance from surveys are assumed to be log-normally distributed so that $N_{j,t}^{\min}$ is calculated as:

$$[4.2] \quad N_{j,t}^{\min} = O_{j,t} e^{Z \sqrt{\log(1+CV_{j,t}^0)^2}}$$

where $O_{j,t}$ is a survey estimate of absolute abundance in area j at time t , $CV_{j,t}^0$ is the coefficient of variation of this estimate, and Z is a standard normal deviate corresponding to a specified percentile (fixed at -0.842 for the 20th percentile following Wade 1998). Eq. 4.2 assumes that $O_{j,t}$ is the median of the log-normal error distribution.

I implemented the PBR management procedure in my operating model by calculating $CL_{j,t}$ immediately after a survey for absolute abundance and using this annual bycatch limit until the next survey.

CLA

Under the CLA procedure the bycatch limit is calculated as a function of population parameter estimates that are derived by fitting a relatively simple, deterministic population model to time-series of estimates of absolute abundance (Cooke 1999). A time-series of bycatch estimates is input to the population model.

The population model of the CLA is:

$$[4.3] \quad N_{j,t} = N_{j,t-1} \left[1 + R_j^{\max} \left(1 - \left[\frac{N_{j,t-1}}{N_j^K} \right]^z \right) \right] - CL_{j,t-1}$$

where $N_{j,t}$ is total population size in area j at time t (years), R_j^{\max} is maximum population growth rate, N_j^K is population size at carrying capacity, and z determines the shape of the density-dependence relationship (fixed at 2). The population model is initialised by assuming that the population is at carrying capacity at $t=0$, the beginning of the bycatch time-series. It is important to note that the population might not have

been at carrying capacity at the beginning of the bycatch time-series, for example if the time-series is incomplete. Nevertheless, the CLA assumes that the population starts at carrying capacity.

The population model is fitted to estimates of absolute abundance using a quasi-Bayesian statistical framework (Cooke 1999, IWC 1999). If errors in estimates of absolute abundance are assumed to be independent over time and log-normally distributed with known $CV(s)$ then a likelihood kernel for non-zero estimates ($L_j^{O \neq 0}$) is:

$$[4.4] \quad L_j^{O \neq 0} = \prod_t^{t \in t_j^{O \neq 0}} e^{-\frac{\left[\log \left(\frac{O_{j,t}}{B_j^O N_{j,t}} \right) \right]^2}{2 \log(1 + CV_{j,t}^{O \neq 0})^2}}$$

where $t_j^{O \neq 0}$ is the set of years in which surveys for absolute abundance were conducted in area j resulting in non-zero estimates of abundance and B_j^O is a bias parameter specifying the expected absolute abundance estimated by a survey as a proportion of true abundance. The CLA procedure also allows for zero estimates of abundance. The likelihood of these estimates is based on the Poisson distribution:

$$[4.5] \quad L_j^{O=0} = \prod_t^{t \in t_j^{O=0}} e^{-\frac{N_{j,t}}{\infty}}$$

where $t_j^{O=0}$ is the set of years in which surveys for absolute abundance in area j resulted in zero estimates and ∞ is the reciprocal of the expected number of animals counted on a survey as a proportion of the number of animals in the population. The value of ∞ depends on various aspects of the surveys (e.g., effort, area covered), but I assumed a theoretical value of 1000. Zero estimates of abundance would have occurred extremely infrequently, if at all, in my simulations. Assuming independence between the zero and non-zero abundance estimates the joint likelihood is the product of Eqs 4.4 and 4.5.

The estimated parameters of the CLA procedure's population model are R_j^{\max} , B_j^O and $D_{j,T}$ (the current number of animals as a proportion of the number of animals at

carrying capacity). Uniform prior probability distributions are assumed for all three parameters: $R_j^{\max} \sim U(0,0.07092)$, $B_j^0 \sim U\left(0, \frac{5}{3}\right)$, and $D_{j,T} \sim U(0,1)$. These prior probability distributions are assumed to be independent.

After each survey for absolute abundance, a posterior distribution of nominal bycatch limits is calculated from the posterior distribution of population model parameters and the corresponding posterior distribution of predicted current population size using a numerical integration algorithm summarized by the following pseudocode:

- I. Start with the minimum R_j^{\max} , maximum N_j^K , and maximum $D_{j,T}$.
- II. If R_j^{\max} is less than the maximum R_j^{\max} then continue to step III, otherwise stop.
- III. Simulate the population from $t=0$ to T using Eq. 4.3 where T is the current year.
- IV. Calculate the new $D_{j,T}$ and the difference between the new $D_{j,T}$ and the previous $D_{j,T}$.
- V. If the new $D_{j,T}$ is ≤ 0 then increment R_j^{\max} and return to step II, otherwise calculate a nominal bycatch limit according to the catch control rule:

$$[4.6] \quad CL_{j,T} = \rho R_j^{\max} N_{j,T} \max \left\{ \min \left(\frac{N_{j,T}}{N_j^K}, 1 \right) - \gamma, 0 \right\}$$

where ρ is a tuning parameter that can be used to adjust the CLA procedure to achieve specific conservation objectives, and γ is a threshold population size relative to carrying capacity at which bycatch is set to zero (the internal protection level).

- VI. Integrate $(L_j^{O \neq 0} \times L_j^{O=0})^w$ over the prior for B_j^0 and multiply by the difference between the new $D_{j,T}$ and the previous $D_{j,T}$ to get a weighted likelihood kernel corresponding to the nominal bycatch limit from step V. The parameter w weights the contribution of the likelihood to the posterior (fixed at 1/16). This

weighting means that this is not a strict Bayesian analysis. The down-weighting is implemented to reduce variability in bycatch limits (Cooke 1999).

VII. Decrement N_j^K and return to step III.

Finally, the set of nominal bycatch limits is sorted and the implemented bycatch limit is chosen to correspond to a specific quantile, Q , of the corresponding cumulative (normalized) weighted likelihoods. I implemented the CLA procedure in the operating model by calculating $CL_{j,t}$ immediately after a survey for absolute abundance and using this annual bycatch limit until the next survey. Time-series of previous bycatch *limits* were input to the CLA procedure.

There were several key differences between my version of the CLA procedure and the version used by the IWC. First, in the IWC version of the catch control rule (Eq. 4.6) R_j^{\max} is replaced by a productivity parameter that is equal to $R_j^{\max}/1.4184$. Thus, ρ in my version of the catch control rule is not equivalent to the corresponding tuning parameter in the IWC version. Second, in the IWC version of the CLA procedure surveys are assumed to have occurred at the start of the last year of catch (or at the start of the last year within an inter-limit period). In my version surveys are assumed to have occurred at the end of the last year of catch (i.e., after the last catch not before). Third, I did not consider covariance among estimates of abundance although covariance is straightforward to incorporate (Cooke 1999).

Operating model

A computer-based simulation model, or operating model, was developed for testing and comparing the performance of the two management procedures and for tuning the procedures so that one would expect to meet the conservation objective in practice. Full specifications of the operating model are described below.

In brief, the operating model simulated a harbour porpoise population over time while periodically simulating surveys of the size of the population. Bycatch was removed from the population annually according to bycatch limits set by the management procedures. Importantly, the management procedures did not have knowledge of the true size of the population, they only had the simulated survey data and bycatch limits as input. This is the key aspect of the simulation model that mimicked how the

management procedures would operate in reality and thus how one would expect populations to fare under the management procedures in practice. The model of the harbour porpoise population incorporated age structure, density dependence in birth rate, multiple subpopulations with dispersal among them, and environmental variation represented by systematic changes in carrying capacity, periodic catastrophic mortality events, and random fluctuations in birth rate. Survey estimates were generated with random error and potentially directional bias. Similarly, bycatch was modelled as a random and potentially biased realization of the set bycatch limit. The operating model allowed for multiple management areas that did not necessarily correspond to the spatial ranges of subpopulations. Thus, the model allowed for flexible spatial scenarios regarding management and subpopulation structure (e.g., seasonal mixing).

The management procedures and operating model were coded using the free software package R (R Development Core Team 2007) and the C computer language compiled with the free MinGW port (<http://www.mingw.org>) of the GNU GCC compiler (<http://www.gnu.org>). I coded the CLA routine in C based on a FORTRAN CLA routine developed and provided by the IWC (1994). I performed many random checks to confirm that my CLA routine gave the same limits as the IWC CLA routine after accounting for the differences described above.

The model of the known population was an age-structured, birth-pulse simulation of one or more subpopulations with a time-step of one year of life. Each subpopulation was modelled individually and during each time-step was subject to four processes in the following order: natural mortality, dispersal, bycatch and reproduction.

First, natural mortality was applied to each subpopulation according to:

$$[4.7] \quad N_{a,i,t} = \text{Binom}(N_{a,i,t}; s_a)$$

where $N_{a,i,t}$ is the number of animals of age a in subpopulation i at time t , s_a is the natural annual survival rate from age a to $a+1$, and $\text{Binom}(n, p)$ is a random binomial variable with sample size n and probability p (see Table 4.1 for a complete list of the parameters of the operating model). The model then allowed for a catastrophic natural mortality event. These events were implemented as 50% mortality across all ages

Table 4.1. Parameters of the operating model and values used in generic performance-testing simulation trials. Baseline values are indicated by ‘*’ and ‘worst-case’ values used for the third tuning are indicated by ‘†’. Fixed parameters were held constant in all trials. In each trial the value of one bottom-level parameter was altered while keeping all others at their baseline values, and then simulations were run over all combinations of values of the top-level parameters.

Parameter(s)	Symbol	Values
<i>Fixed</i>		
Age at which 50% of animals are sexually mature	a^{m50}	4*
Width of maturity ogive	σ^m	0.5*
Maximum age	ω	20*
Age-specific vulnerability to bycatch	η_a	1* (for all a)
Age-specific natural annual survival rate	s_a	0.85* for $0 < a < 4$, 0.925* for $a \geq 4$
Total number of animals at carrying capacity in each subpopulation	$\sum_{a=0}^{\omega} N_{a,i,t}^K$	100000*

Table 4.1 contd.

Parameter(s)	Symbol	Values
<i>Top-level</i>		
Initial population status (number of non-calves in each subpopulation as proportion of the number at carrying capacity)	$D_{i,0}$	Two sets of trials (only the first set was done with the PBR procedure): 1)* 15 years of constant bycatch ($CL_{j,t}$) prior to the simulation period resulting in $\frac{\sum_{a=0}^{\omega} N_{a,i,t=0}}{\sum_{a=0}^{\omega} N_{a,i,t}^K} = 0.05$, 0.1, 0.3, 0.6, 0.8 and 0.99 2) $\frac{\sum_{a=0}^{\omega} N_{a,i,t=0}}{\sum_{a=0}^{\omega} N_{a,i,t}^K} = 0.05, 0.1, 0.3, 0.6, 0.8, \text{ and } 1$ and a historical bycatch of 1 animal for one year
Maximum birth rate	b^{\max}	0.284931, 0.350061* (result in maximum annual population growth rates of 2% and 4%, respectively)
<i>Bottom-level</i>		
Shape of density dependence	z	0.1, 1*, 13.5 (result in maximum net productivity levels of about 40%, 50% and 85% of carrying capacity, respectively)
Survey bias (expected estimated absolute abundance as proportion of true absolute abundance)	B^0	0.5, 1*, 1.5 [†]
Survey precision (CV of estimates of absolute abundance)	CV^0	0.1, 0.2*, 0.6 (for $B^{CV^0} = 1$ and 2)

Table 4.1 contd.

Parameter(s)	Symbol	Values
<i>Bottom-level</i>		
Survey CV bias (true CV of estimates of absolute abundance as proportion of estimated CV of these estimates)	B^{CV^0}	0.5, 1, 2*
Bycatch bias (realized bycatch as proportion of bycatch limit)	B^{byc}	0.5, 1*, 2†
Bycatch precision (CV of realized bycatch)	CV^{byc}	0.1, 0.3*, 1.0
Survey frequency	f	5, 10*, 15
Change in carrying capacity	$\sum_{a=0}^{\omega} N_a^K$	no change*, 50% linear increase or decrease over simulation period
Catastrophes (annual probability of catastrophic natural mortality)	$P^{catastrophe}$	0*, 0.02
Environmental stochasticity (CV of birth rate deviations)	CV^{env}	0*, 0.2
Environmental stochasticity (autocorrelation in birth rate deviations)	ϕ	0*, 0.5 (when $CV^{env}=0.2$)

Table 4.1 contd.

Parameter(s)	Symbol	Values
<i>Population structure</i>		
Number of subpopulations	I	1*
Number of management areas	J	1*
Proportion of subpopulation in management area (surveys)	$\beta_{j,i}^{\text{srvy}}$	1*
Proportion of subpopulation in management area (bycatch)	$\beta_{j,i}^{\text{byc}}$	1*
Dispersal rate	δ_i	NA

(subject to demographic stochasticity) after the usual natural mortality. These events occurred with a specified probability each year ($P^{\text{catastrophe}}$). Although it would have been more realistic to represent catastrophes as extreme events in a continuous distribution of environmental variability (Reed et al. 2003), I modelled catastrophic events as a separate process to examine the impact of relatively frequent catastrophes.

Second, the survivors of natural mortality dispersed between subpopulations according to:

$$[4.8] \quad N_{a,i,t} = N_{a,i,t} - \text{Binom}(N_{a,i,t}; \delta_i) + \text{Binom}(N_{a,k,t}; \delta_k)$$

where δ_i and δ_k are the rates of dispersal from subpopulations i and k , respectively ($i \neq k$). δ_i and δ_k were assumed to be the same for all ages. Eq. 4.8 is only appropriate for a population composed of two subpopulations. Note that because natural mortality rates did not vary by density or subpopulation, the order of natural mortality and dispersal did not affect dynamics.

Third, bycatch was removed from the population. Total bycatch from the population in management area j during the year following time t ($TC_{j,t}$) was modelled as a potentially biased, random deviation from the set bycatch limit for year t ($CL_{j,t}$):

$$[4.9] \quad TC_{j,t} = B^{\text{byc}} \text{N}(CL_{j,t}, [CL_{j,t} CV^{\text{byc}}]^2)$$

where B^{byc} is the directional bias in actual bycatch relative to the bycatch limit (expected $TC_{j,t}$ as a proportion of $CL_{j,t}$), CV^{byc} is the coefficient of random variation in bycatch and $\text{N}(\mu, \sigma^2)$ is a random normal variable with expectation μ and variance σ^2 . Random deviations from the bycatch limit were assumed to be independent between years. The expected proportion of the bycatch composed of animals of age a from subpopulation i in management area j during the year following time t ($v_{a,i,j,t}$) was calculated according to:

$$[4.10] \quad v_{a,i,j,t} = \frac{\eta_a \beta_{j,i}^{\text{byc}} N_{a,i,t}}{\sum_{a=0}^{\omega} \sum_{i=1}^I \eta_a \beta_{j,i}^{\text{byc}} N_{a,i,t}}$$

where η_a is the vulnerability of an animal of age a to bycatch relative to other ages, $\beta_{j,i}^{\text{byc}}$ is the proportion of subpopulation i residing in management area j during bycatch, ω is maximum age, and I is the total number of subpopulations. The calculation of vulnerabilities (Eq. 4.10) assumed that all animals within a management area mixed freely irrespective of age and subpopulation. The total bycatch in area j was then distributed stochastically among the subpopulations and ages within subpopulations according to:

$$[4.11] \quad \mathbf{C}_{j,t} = \text{Multin}(TC_{j,t}; \mathbf{V}_{j,t})$$

where $\mathbf{C}_{j,t} = [c_{a,i}]_{j,t}$ is the matrix of bycatch c of age a from subpopulation i in management area j during the year following time t , $\mathbf{V}_{j,t} = [v_{a,i}]_{j,t}$ is the matrix of proportions of bycatch, and $\text{Multin}(n; \mathbf{p})$ represents a random multinomial distribution with sample size n and probabilities \mathbf{p} . Note that $\sum_{a=0}^{\omega} \sum_{i=1}^I v_{a,i,j,t} = 1$. The age- and subpopulation-specific bycatch was then removed while incrementing ages by one year according to:

$$[4.12] \quad N_{a+1,i,t+1} = \max\left(N_{a,i,t} - \sum_{j=1}^J c_{a,i,j,t}, 0\right) \quad \text{for } a < \omega$$

where J is the total number of management areas. Note that removing bycatch after natural mortality maximized the overall mortality rate for a given absolute bycatch because all bycaught animals were survivors of natural mortality.

The only calf mortality resulting from bycatch (Eqs 4.9-4.12) was calves bycaught according to their age-specific vulnerability. However, if lactating females with dependent calves are bycaught then their abandoned calves will die, but potentially not be a part of the bycatch. The maximum additional calf mortality from subpopulation i in year t that could result from abandonment might be:

$$[4.13] \quad \left(1 - \frac{\sum_{j=1}^J c_{0,i,j,t}}{N_{0,i,t}}\right) b_{i,t} \sum_{j=1}^J \sum_{a=1}^{\omega} c_{a,i,j,t} m_{a-1}$$

which assumes that calves are entirely dependent on their mothers for their first year of life (i.e., the calf of a bycaught mother will die) and that the probability of a calf being bycaught is independent of the probability of the mother being bycaught. Similar assumptions were made by Woodley (1993) in a modelling study of dolphin bycatch. The latter assumption seems unlikely because mothers and calves would be together and thus experience similar risks of bycatch. Nevertheless, I explored the effect of calf abandonment (according to Eq. 4.13) on the performance of the management procedures.

Fourth, reproduction was applied:

$$[4.14] \quad N_{0,i,t} = \text{Binom} \left[\sum_{a=1}^{\omega} (N_{a,i,t} m_{a-1}), b_{i,t} \right]$$

where m_a is the proportion of animals that are sexually mature at age a and b is annual birth rate (number of calves per mature animal). The sexual maturity ogive was:

$$[4.15] \quad m_a = \left(1 + e^{\frac{a-a^{m50}}{\sigma^m}} \right)^{-1}$$

where a^{m50} is the age at which 50% of animals are sexually mature and σ^m is a parameter determining the width of the maturity ogive. Note that maturity was not treated stochastically in order to simplify computation; in Eq. 4.14 the term $N_{a,i,t} m_{a-1}$ was rounded to the nearest integer. The main assumptions regarding natural mortality and reproduction were: 1) females could potentially give birth for the first time one year after they matured; 2) b did not vary with age; and 3) all animals died before $t=\omega+1$ (knife-edge survival senescence).

Birth rate was assumed to be density-dependent and a function of the number of non-

calves ($\sum_{a=1}^{\omega} N_{a,i,t}$):

$$[4.16] \quad b_{i,t} = \min \left\{ \max \left\{ b^K + (b^{\max} - b^K) \left[1 - \left(\frac{\sum_{a=1}^{\omega} N_{a,i,t}}{\sum_{a=1}^{\omega} N_{a,i,t}^K} \right)^z \right], 0 \right\}, e^{\varepsilon_t}, 0.5 \right\}$$

where b^{\max} is maximum birth rate, b^K is birth rate at carrying capacity, $\sum_{a=1}^{\omega} N_{a,i,t}^K$ is the number of non-calves in subpopulation i at carrying capacity at the beginning of year t , z is a density-dependence shape parameter, and ε_t is a random deviation in birth rate in year t as a result of environmental variability. It was ensured that the expected birth rate was greater than zero and that realized birth rate was less than 0.5. Note that the number of calves born at the beginning of year t was a function of the number of non-calves at the beginning of year t (Witting and Born 2005). Alternatively, I could have made the number of calves born at the beginning of year t a function of the number of non-calves at the beginning of the previous year (Skaug et al. 2008), which would have been more similar to the population model of the CLA procedure. These two formulations give identical equilibrium populations with or without harvest; the only effect on my results would have been negligible differences in recovery time from a given initial population.

Birth rate at carrying capacity was calculated as:

$$[4.17] \quad b^K = \left(\sum_{a=1}^{\omega} l_a m_{a-1} \right)^{-1}$$

where l_a is survivorship to age a . Survivorship was calculated as:

$$[4.18] \quad l_a = \begin{cases} 1 & \text{for } a = 0 \\ \prod_{x=0}^{a-1} s_x & \text{for } a > 0 \end{cases}$$

The number of non-calves at carrying capacity was not treated as a parameter, it was calculated from a parameter specifying the total number of animals at carrying

capacity ($\sum_{a=0}^{\omega} N_{a,i,t}^K$) using the following relationship:

$$[4.19] \quad \sum_{a=1}^{\omega} N_{a,i,t}^K = \sum_{a=0}^{\omega} N_{a,i,t}^K \left[1 - \left(\sum_{a=0}^{\omega} l_a \right)^{-1} \right]$$

I also allowed for linear changes in the number of animals at carrying capacity over time.

In addition to density dependence in birth rate, the operating model allowed for stochastic annual variation in birth rate over time representing environmental variability. Annual multipliers of birth rate were assumed to be log-normally distributed and potentially correlated over time (first-order autoregressive model) with mean 1 and coefficient of variation CV^{env} so that:

$$[4.20] \quad \varepsilon_t = -0.5 \log(1 + CV^{\text{env}^2}) (1 - \varphi) + \varphi \varepsilon_{t-1} + N\left[0; \log(1 + CV^{\text{env}^2}) (1 - \varphi^2)\right]$$

where $|\varphi| < 1$ is a parameter controlling the strength of the correlation in deviations over time ($\varphi = 0$ specifies no correlation). The first deviation was initialised to the mean value:

$$[4.21] \quad \varepsilon_0 = -0.5 \log(1 + CV^{\text{env}^2})$$

Note that stochastic variation in vital rates can alter mean properties of population dynamics such as long term growth rate (Lande 1993). In my density-dependent model, stochastic variation in birth rate likely altered the maximum sustainable bycatch rate and its corresponding equilibrium population size although these effects might have been small (Punt 2008).

Immediately after births, survey estimates of absolute abundance ($O_{j,t}$) were simulated for each management area every f years for input to the management procedure. First, animals were distributed stochastically among management areas according to:

$$[4.22] \quad \mathbf{X}_{i,t} = \text{Multin}\left(\sum_{a=0}^{\omega} N_{a,i,t}; \boldsymbol{\beta}_i^{\text{srvy}}\right)$$

where $X_{i,t}=[x_j]_{i,t}$ is the vector of numbers of animals in management areas j belonging to subpopulation i at time t , and $\beta_i^{\text{srvy}} = [\beta_j^{\text{srvy}}]_i$ is the vector of expected proportions of animals belonging to subpopulation i in management areas j at the time of surveys. Survey estimates were then simulated for each management area assuming that the errors in the estimates were independent between years and surveys and log-normally distributed so that:

$$[4.23] \quad O_{j,t} = e^{\text{N}\left[\log\left(B^0 \sum_{i=1}^I x_{j,i,t}\right), \log\left(1 + (B^{\text{cv}0} \text{CV}^0)^2\right)\right]}$$

where B^0 is a directional bias parameter specifying the expected absolute abundance estimated by a survey as a proportion of true abundance, and $B^{\text{cv}0}$ is a directional bias parameter specifying the true coefficient of variation in survey estimates of absolute abundance as a proportion of the estimated coefficients of variation of the estimates of absolute abundance. Eq. 4.23 assumes that the true population size is the median of the log-normal error distribution which is identical to the assumed error distribution for abundance estimates in the PBR and CLA procedures (Eqs 4.2 and 4.4, respectively). Note that performance-testing simulations of the PBR procedure presented in Wade (1998) assumed that the true population size was the mean of the lognormal distribution for simulating survey estimates.

Simulations were initialized by first setting the number of non-calves in subpopulation i to a proportion of the number of non-calves in that subpopulation at carrying capacity ($D_{i,0}$):

$$[4.24] \quad \sum_{a=1}^{\omega} N_{a,i,0} = D_{i,0} \sum_{a=1}^{\omega} N_{a,i,0}^K$$

Then $b_{i,0}$ was calculated according to Eq. 4.16. Next, the age distribution at $t=0$ for each subpopulation was set to the stable age distribution (dominant eigenvector of the transition matrix) specified by deterministic versions of Eqs 4.7 and 4.14 with $b_{i,0}$. Finally, the number of animals of each age at $t=0$ were calculated from this age distribution and $\sum_{a=1}^{\omega} N_{a,i,0}$. Such a stable age distribution would of course not be realized in a population governed by density-dependent dynamics. Nevertheless, this

age distribution was used to represent more realistic age distributions for subpopulations that were initially at fractions of their carrying capacity. Note that while the population model of the CLA procedure assumes that the population is at carrying capacity at the beginning of the bycatch time-series, this does not have to be the case in the operating model.

Tuning of the management procedures

I used the operating model to tune the management procedures so that one would expect to achieve the conservation objective in practice. As described above, three different tunings were developed. All three tunings were based on a single subpopulation inhabiting a single management area. The operating model was used to simulate this subpopulation subject to bycatch as limited by the management procedures for a period of 200 years. Population status at the end of the 200-year simulation period was examined to determine whether the conservation objective was achieved. If the objective was not achieved then the values of the tuning parameters of the management procedures were adjusted and the simulation was run again. This process was iterated until the conservation objective was achieved. In its original development by the IWC, the CLA procedure was tuned by fixing the values of the tuning parameters ρ and γ and adjusting the value of Q . Aldrin et al. (2006, 2008) advocated fixing Q at 0.5 and adjusting ρ to tune the CLA. They pointed out that it was impossible to tune the CLA to achieve final depletions <0.7 over a 300-year timeframe when ρ and γ were fixed at their default tuned values. This was because with infinite data the posterior distribution of nominal bycatch limits is degenerate to a single value and is therefore not affected by Q . I chose to use ρ to tune the CLA following Aldrin et al. (2008). However, I fixed Q at 0.4 to maintain the conservative feature that greater variance in the posterior distribution of nominal bycatch limits (for example because of greater uncertainty in abundance estimates) resulted in a lower bycatch limit. The internal protection threshold, γ , was set to 0.5, the assumed maximum net productivity level in my base model ($z=1$).

The tunings of the management procedures presented here have relatively low precision compared to tunings of the CLA procedure developed by the IWC (e.g., IWC 2002). However, the precision does not affect the relevance of my results.

Higher precision tunings could be performed when a management procedure is finalised.

The first tuning was developed in a manner similar to the tuning of the CLA procedure by the IWC. All parameters of the operating model were set at their baseline values (Table 4.1). Initial population status (population size as a proportion of carrying capacity) was set to 0.99. For the CLA procedure a 15-year historical time-series of bycatch was assumed that reduced the population to 99% of carrying capacity at the beginning of the simulation period. Maximum population growth rate was assumed to be 4% per year with a density-dependence relationship that resulted in maximum net productivity at 50% of carrying capacity. These population parameter values were considered to be conservative for harbour porpoise and were chosen based on the suggestions of the IWC/ASCOBANS working group (IWC 2000). The management procedures were then tuned under this scenario so that the median population status after 200 years was 80%. This tuning is therefore appropriate for a conservation objective of maintaining the population *at* 80% of carrying capacity in the long term.

The second tuning was developed in exactly the same way except that the management procedures were tuned so that there was a 95% probability that population status was $\geq 80\%$ of carrying capacity after 200 years. This is similar to the way in which the PBR procedure was tuned in its original development except in that case the objective was $\geq 50\%$ of carrying capacity, the lower limit of the range 50-70% (Wade 1998). This tuning is therefore appropriate for a conservation objective of maintaining the population *at or above* 80% of carrying capacity in the long term.

The third tuning was developed considering a worst-case scenario. Population parameter values were identical to those used in the first two tunings and all parameters of the operating model were set at their baseline values except two. Exploratory simulations indicated that the two parameters with the largest effects on performance (other than maximum population growth rate and maximum net productivity level) were bias in survey estimates of population size and bias in estimates of bycatch. Worst-case values for the above parameters were chosen as follows. A 50% overestimate was chosen as the worst-case bias in absolute estimates of population size. It was assumed that future surveys would be conducted using a

methodology similar to the Small Cetaceans of the European Atlantic and North Sea - II survey (SCANS-II 2008); this was a robust, design-unbiased methodology that was highly unlikely to systematically overestimate population size by more than 50%. A 50% underestimate was chosen as the worst-case bias in estimates of future bycatch (i.e., actual bycatch would be twice the estimated bycatch). The estimation of bycatch is fraught with uncertainty, but this tuning of the procedures assumed that estimates of bycatch in the future would by design not underestimate bycatch by more than 50%. Initial population statuses ranging from 0.05-1.00 were considered for this tuning. The management procedures were then tuned so that there was a 95% probability that population status was ≥ 0.80 after 200 years (under this worst-case scenario). This tuning is therefore appropriate for a conservation objective of maintaining the population *at or above* 80% of carrying capacity in the long term *under a worst-case scenario*.

Performance of the management procedures beyond 200 years was not examined.

Performance-testing simulations

To assess the robustness of the tuned PBR and CLA procedures a series of performance-testing simulation trials were conducted using the operating model. These trials were intended to be generic and thus covered a wide range of uncertainties. The simulations were of a single subpopulation inhabiting a single management area over 200 years. All parameters were set at their baseline values (Table 4.1) except the parameter of interest in a given trial. Table 4.1 shows the ranges of parameter values explored in these trials. The performance of the management procedures was examined with respect to uncertainty in initial population status, maximum population growth rate, shape of density dependence, survey precision and bias, bycatch precision and bias, survey frequency and environmental variability.

All simulations were conducted for two maximum population growth rates (2% and 4%) and for a range of initial population statuses (0.05, 0.10, 0.30, 0.60, 0.80 and 0.99). Two sets of simulation trials were conducted with respect to initial population status and historical bycatch. In the first set of trials a population at carrying capacity was subjected to 15 years of bycatch prior to the 200-year simulation period to

achieve the desired initial population status. This historical time-series of bycatch was input to the CLA procedure. The non-linear minimization routine ‘optimise’ in R (R Development Core Team 2007) was used to calculate the constant annual historical bycatch that would achieve the desired initial population status given a specific maximum birth rate and shape of density dependence. The second set of trials was only conducted for the CLA procedure. In these trials I essentially assumed that no information was available on historical bycatch, even if the population was not at carrying capacity. In order for the CLA procedure to operate I had to use a historical bycatch of one animal for one year prior to the start of the simulation period. The optimise function was used to calculate the appropriate values of D_0 (Eq. 4.24) for initial total population statuses of 0.05, 0.1, 0.3, 0.6, 0.8 and 1.0 and it was assumed that the population was at this status prior to the historical bycatch of one animal for one year.

Seven performance metrics were examined in the simulation trials:

- 1) Total bycatch limits during the 200-year simulation period as a proportion of carrying capacity:

$$[4.25] \quad \text{Tot. Byc. Limit/K} = \frac{\sum_{t=0}^{199} CL_t}{\sum_{a=0}^{\omega} N_{a,t=0}^K}$$

- 2) Final population size as a proportion of carrying capacity:

$$[4.26] \quad \text{Final N/K} = \frac{\sum_{a=0}^{\omega} N_{a,t=200}}{\sum_{a=0}^{\omega} N_{a,t=0}^K}$$

- 3) Lowest population size during the simulation period as a proportion of carrying capacity:

$$[4.27] \quad \text{Lowest N/K} = \min \left(\frac{\sum_{a=0}^{\omega} N_{a,t}}{\sum_{a=0}^{\omega} N_{a,t=0}^K} \right) \quad \text{for } t = 0 \text{ to } 200$$

- 4) Realized protection level (lowest population status during the simulation period in years when bycatch was >0):

$$[4.28] \quad \text{RPL} = \min \left(\frac{\sum_{a=0}^{\omega} N_{a,t}}{\sum_{a=0}^{\omega} N_{a,t=0}^K} \right) \quad \text{for } t = 0 \text{ to } 200 \text{ where } TC_t > 0$$

- 5) Average annual bycatch limit variability during simulation period:

$$[4.29] \quad \text{AABV} = \frac{\sum_{t=0}^{198} |CL_{t+1} - CL_t|}{\sum_{t=0}^{198} CL_t}$$

AABV is equivalent to the mean absolute annual change in bycatch limit as a proportion of the mean bycatch limit. It is not the mean proportional annual change in bycatch limit. The former is a more appropriate measure of variability when the magnitude of absolute changes in bycatch limit is of more interest than the magnitude of proportional changes in bycatch limit. For example, the following two series of bycatch limits: {1,10,1,10,10} and {10,1,10,1,1} have the same AABV, but the first series has a higher mean proportional annual change in bycatch limit.

- 6) Absolute delay in recovery to 80% of carrying capacity (in years) relative to an identical scenario without bycatch (or delay in recovery to the population status at the end of the simulation period in the scenario without bycatch):

$$[4.30] \quad \text{Abs. Recovery} = t^{\text{target}} - t_{\text{CL}=0}^{\text{target}}$$

where

$$[4.31] \quad \text{target} = \min \left(0.8, \frac{\sum_{a=0}^{\omega} N_{a,t=200}}{\sum_{a=0}^{\omega} N_{a,t=0}^K} \right) \quad \text{when all } CL_t = 0$$

and

$$[4.32] \quad t^{\text{target}} = \min(t) \quad \text{where} \quad \frac{\sum_{a=0}^{\omega} N_{a,t}}{\sum_{a=0}^{\omega} N_{a,t=0}^K} \geq \text{target}$$

and $t_{\text{CL}=0}^{\text{target}}$ is calculated in the same way as t^{target} for an identical scenario without bycatch (bycatch limits set to zero). The target and $t_{\text{CL}=0}^{\text{target}}$ were calculated using median population sizes from simulations without bycatch. The median recovery delay and 90% probability interval were calculated using Eq. 4.32 with median and 90% interval population sizes, respectively. This metric is not relevant for initial population statuses ≥ 0.80 . Note that in the absence of bycatch populations would not necessarily recover to 80% of carrying capacity within 200 years, if at all (e.g., low maximum population growth rate or environmental change).

- 7) Relative delay in recovery to 80% of carrying capacity relative to an identical scenario without bycatch (or delay in recovery to the population status at the end of the simulation period in the scenario without bycatch):

$$[4.33] \quad \text{Rel. Recovery} = \frac{\text{Abs. Recovery}}{t_{\text{CL}=0}^{\text{target}}}$$

This metric is not relevant for initial population statuses ≥ 0.80 .

My version of the CLA procedure had relatively low-precision numerical integration compared to the final version of the CLA procedure developed by the IWC, however, performance in my trials should be similar to that in trials of a more precise version (IWC 2002). I ran some trials with a higher precision version of the CLA procedure and the results were very similar to those obtained with the lower precision version. Furthermore, the behaviour of my version of the CLA procedure was qualitatively similar to the behaviour of the CLA procedure in similar, higher-precision simulation trials by Aldrin et al. (2006).

Multi-subpopulation simulations

The operating model allowed for simulations of multiple subpopulations and management areas. The parameters that were particularly relevant to multi-subpopulation/management area scenarios included the number of subpopulations (I),

the number of management areas (J), the proportion of each subpopulation in each area during surveys ($\beta_{j,i}^{\text{srvy}}$) and bycatch ($\beta_{j,i}^{\text{byc}}$), dispersal rate from each subpopulation (δ_i), carrying capacity of each subpopulation ($\sum_{a=0}^{\omega} N_{a,i,t}^K$), and initial status of each subpopulation ($D_{i,0}$). These parameters allow for a wide range of simulation scenarios with respect to population structure and movement and spatial management. For example, one could explore the performance of a management procedure applied separately to individual subpopulations linked by dispersal of various magnitudes and symmetry (e.g., source-sink dynamics, rescue effects). One could also explore the performance of a management procedure applied separately to individual management areas that do not necessarily correspond to the ranges of subpopulations. This situation could arise if population structure is unknown and management areas straddle subpopulation boundaries or if animals from different subpopulations inhabit the same areas during all or part of the year (e.g., seasonal mixing).

I conducted an example set of simulations to illustrate the performance of the first tuning of the management procedures in multi-subpopulation/management area scenarios. Three hypothetical scenarios (A-C) were simulated. In all three scenarios, the population was composed of two distinct subpopulations. It was assumed that the carrying capacity for each of these two subpopulations was 100,000 animals and that the initial size of each subpopulation was 60,000. All other parameters were set to their baseline values. In Scenario A the subpopulations were managed with two separate management areas whose boundaries corresponded to the ranges of the subpopulations. In Scenario B the subpopulations were managed with one management area encompassing the ranges of both subpopulations, but the second subpopulation was twice as vulnerable to bycatch as the first subpopulation, for example because of more fishing effort in the range of the second subpopulation. Scenario C was identical to Scenario B with the exception that each subpopulation had a dispersal rate of 5% per year.

Implementation for harbour porpoise in the North Sea

I calculated bycatch limits and evaluated the performance of the tuned management procedures for harbour porpoise in the North Sea.

The PBR and CLA management procedures require at least one estimate of current abundance. An estimate of harbour porpoise abundance in the North Sea was available for summer 2005 as described in Chapter 3 (216,415, CV=0.20). Estimates were also available for northern and southern sub-areas of the North Sea: 91,175 (0.22) and 125,240 (0.21), respectively (Chapter 3, Fig. 3.1). Bycatch limits for the entire North Sea and for the northern and southern sub-areas were calculated with the PBR procedure using these abundance estimates.

The CLA management procedure can also take historical estimates of abundance and bycatch as input. Historical estimates of harbour porpoise abundance in the North Sea were available for summer 1994: 265,606 (CV=0.16) for the entire North Sea and 190,028 (0.17) and 75,578 (0.20) for the northern and southern sub-areas, respectively (Chapter 3). The integrated population dynamics model described in Chapter 3 provided time-series of historical bycatch estimates for the North Sea (Table 4.2). Bycatch limits for the entire North Sea were calculated with the CLA procedure using median estimates of bycatch from Scenario 1 (single population, density-independent dynamics), along with the historical and current estimates of abundance. Median estimates of bycatch from Scenario 9 (two sub-populations, density-independent dynamics, linearly increasing rate of dispersal from the north to south) were used as input to the CLA procedure for calculating bycatch limits for the northern and southern sub-areas of the North Sea.

The density-dependent Scenario 6 of the integrated population dynamics model presented in Chapter 3 was very similar to the operating model used to test the management procedures. Thus, the joint posterior probability distribution from the integrated model provided distributions of parameter values and distributions of historical time-series of bycatch that could be used for further performance-testing simulations of the management procedures conditioned on the results of the integrated model. I conducted performance-testing simulations of each of the three tunings of the PBR and CLA management procedures conditioned on the joint posterior probability distribution from Scenario 6 of the integrated model. Ten thousand forward simulations were conducted for 200 years beginning in the middle of 2005 (i.e., the beginning of a year in the operating model). The simulation modelled the entire North Sea as a single population inhabiting a single management area. Each simulation was

Table 4.2. Time-series of historical bycatch input to the CLA procedure to calculate bycatch limits for harbour porpoise in the North Sea (Table 4.3). Year represents the year of life beginning in the year indicated (e.g., 1987 would represent 1 July 1987 – 30 June 1988). Bycatches for the entire North Sea are median estimates from Scenario 1 of the integrated population dynamics model presented in Chapter 3; bycatches for the northern and southern sub-areas are from Scenario 9. Note that estimates of bycatch for the northern and southern North Sea do not necessarily sum to the estimates for the entire North Sea as these sets of estimates are from different model scenarios.

Area	Year																	
	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
North Sea	10644	9964	9422	10615	11529	11298	11169	10686	9265	7974	7052	6030	5159	4726	4496	3811	3278	3196
Northern North Sea	6154	5862	5616	6136	6108	6064	5548	4654	4089	3443	2855	2473	1936	1399	1130	839	567	383
Southern North Sea	3483	3623	3864	4663	5664	6128	6392	6512	5888	5352	5328	4918	4519	4395	4376	4067	3829	4086

based on one set of parameter values and the corresponding historical time-series of bycatch from the joint posterior probability distribution. Operating model parameters that were not in the integrated model (e.g., future survey frequency, precision, etc.) were set to their baseline values (Table 4.1). Under the PBR procedure the 2005 estimate of abundance was used to calculate the first bycatch limit and under the CLA procedure the 1994 abundance estimate and the historical time-series of bycatch were also used to calculate the first bycatch limit.

There are at least four important differences between the integrated model and the operating model. First, annual estimates of bycatch from the integrated model correspond to *calendar years* while the operating model takes as input annual estimates of bycatch corresponding to *years of life*. Historical estimates of bycatch for years of life in the operating model were approximated by assuming that calendar-year estimates of bycatch were evenly distributed throughout the year (Table 4.2). Second, the integrated model was deterministic while the operating model is stochastic. Third, birth rate is a function of the number of non-calves at the *beginning* of the calendar year in the integrated model, but birth rate is a function of the number of non-calves at the *middle* of the calendar year in the operating model. Fourth, natural and bycatch mortality occur concurrently throughout the year in the integrated model while bycatch is removed after natural mortality in the operating model. Thus, a given absolute bycatch will have a greater impact in the operating model than in the integrated model for the same natural mortality rate. These differences result in somewhat inconsistent inference between the historical period (integrated model) and the future period (operating model). The difference in the relative timing of natural and bycatch mortality results in the greatest difference in dynamics. Nevertheless, the differences in dynamics arising from differences between the integrated and operating models were very small relative to the differences in dynamics arising from the variation in parameter values from the posterior distribution. Thus, the general results of the conditioned performance-testing simulations were robust to the inconsistencies between the integrated and operating models.

Results

Tuning of the management procedures

The three tunings of the procedures performed quite differently in terms of the conservation objective (long-term population status) and recovery delay (Figs 4.1 and 4.2). With the first tuning, PBR1 and CLA1, the population was maintained at 80% of carrying capacity, as defined by the objective. In the second tuning, PBR2 and CLA2, the population was maintained at a higher percentage of carrying capacity (~85-90%) because of the requirement to achieve the conservation objective 95% of the time. In the third tuning, PBR3 and CLA3, the population was maintained at an even higher percentage of carrying capacity (~95%) because of the additional requirement to achieve the conservation objective under a worst-case scenario.

Under the PBR procedure, median bycatch limits were approximately a constant proportion of population size. Therefore, changes in median population size were monotonic, the population reached a long-term equilibrium status that was independent of the initial population status (Figs 4.1 and 4.2), and the delay in recovery to 80% of carrying capacity, relative to a scenario without bycatch, was longer for lower initial population statuses (Fig. 4.1). As expected, long-term population status was highest and delay in recovery was shortest under the third tuning of the PBR procedure (Fig. 4.1). The values of the tuning parameter (F) for the three tunings of the PBR procedure were 0.46, 0.34 and 0.11, respectively.

Under the CLA procedure median bycatch limits varied as a proportion of population size so changes in median population size were not always monotonic (Fig. 4.2). Population status did not always equilibrate within 200 years, even for populations that were not heavily depleted (Fig. 4.2). Population status at 200 years varied depending on initial population status (Fig. 4.1). Long-term population status was highest and delay in recovery was shortest under the third tuning of the CLA procedure (Fig. 4.1). The values of the tuning parameter (ρ) for the three tunings of the CLA procedure were 2.95, 1.71 and 0.43, respectively.

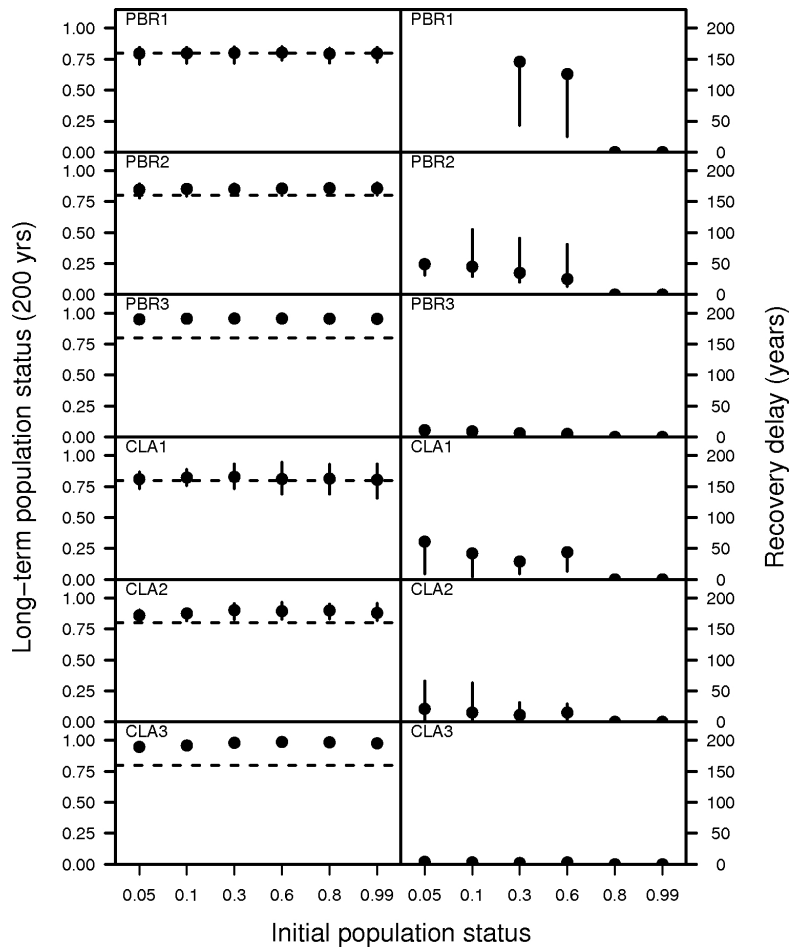


Figure 4.1. Performance of three tunings of the PBR and CLA management procedures under the baseline scenario with respect to the conservation objective (long-term population status) and recovery delay. Points represent median results from 100 simulations and error bars represent the 90% interval of simulation outcomes. Population status is defined as population size as a proportion of carrying capacity. The horizontal dashed lines indicate the conservation objective: population status = 0.80. Recovery delay is defined as the delay in recovery of a population to 80% of carrying capacity relative to a scenario without bycatch.

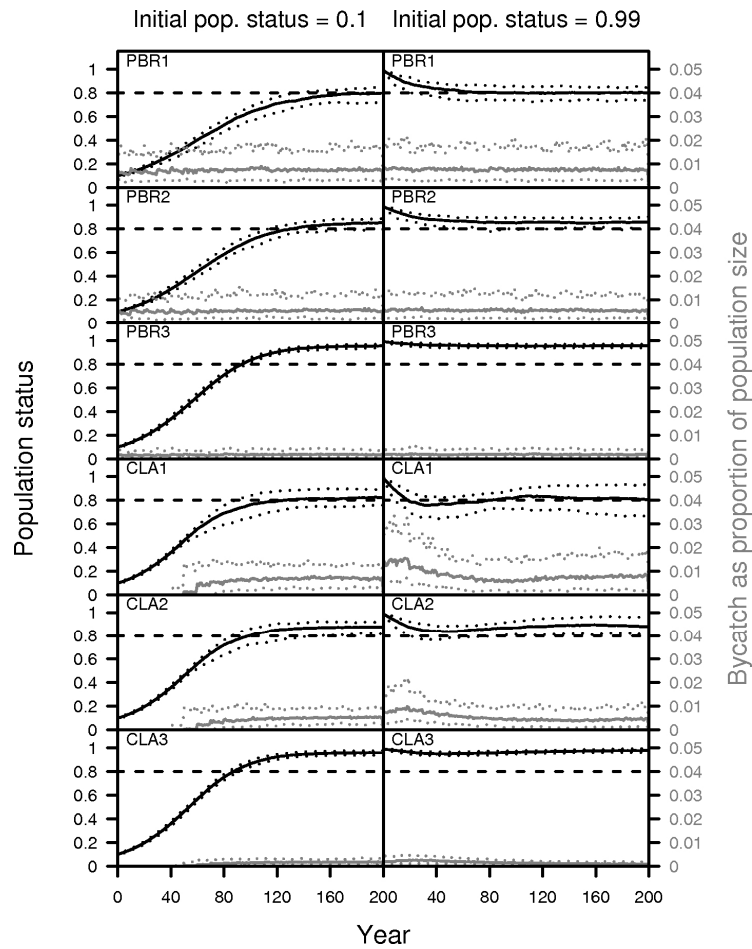


Figure 4.2. Trajectories of population status and bycatch (as proportion of population size) for three tunings of the PBR and CLA management procedures under the baseline scenario. Population status is defined as population size as a proportion of carrying capacity. Results are shown for two initial population statuses: 0.10 (left column) and 0.99 (right column). Solid lines represent median results from 100 simulations and dotted lines represent the 90% interval of simulation outcomes. The horizontal dashed lines indicate the conservation objective (population status = 0.80).

The delay in recovery of depleted populations to 80% of carrying capacity under the CLA procedure tended to be shorter than under the PBR procedure for a given tuning and initial population status (Fig. 4.1). The internal protection mechanism of the CLA procedure resulted in no bycatch when the population was highly depleted allowing faster short-term recovery (Fig. 4.2).

Variability in final population status among simulations was similar between the CLA and PBR procedures when initial population status was low (≤ 0.1). However, variability in final population status was higher under the first and second tunings of the CLA procedure than under the same tunings of the PBR procedure when initial population status was higher. For example, when initial population status was 0.99 the CV of final population status was 0.09 and 0.05 under the first and second tunings of the CLA procedure, respectively, and 0.05 and 0.03 under the first and second tunings of the PBR procedure (Fig. 4.2).

Performance-testing simulations

Detailed results of the performance-testing simulations of the management procedures are presented in an appendix on the supplementary compact disc included with this thesis (PDF file named 'Appendix').

First and second tunings

The simulation trials revealed scenarios that could result in unsatisfactory performance of the first and second tunings of the management procedures, that is in these cases the procedures did not allow the conservation objective to be fully met. Two scenarios that resulted in long-term population status substantially less than the conservation objective were a 50% overestimation of abundance, and a 50% underestimation of bycatch. These two scenarios correspond to the worst-case scenario. By definition, the worst-case scenario has lower plausibility than the baseline scenario. To examine the generality of my tunings (e.g., for other species) I also explored scenarios where the maximum population growth rate was 2% per year and the maximum net productivity was at a population status $< 50\%$ ($z = 0.1$). These scenarios also resulted in long-term population status substantially less than the conservation objective. As discussed above, I considered a maximum population growth rate of 4% and a maximum net productivity at a population status of 50% to

be conservative for harbour porpoise, with lower values having low plausibility. The first and second tunings are not appropriate for achieving the conservation objective for species with lower maximum population growth rates and maximum net productivity levels. Note that although the CLA procedure estimates the maximum population growth rate and bias in survey estimates, bycatch limits set by the CLA procedure did not fully compensate for differences in these parameters. The assumed prior probability distributions and down-weighting of the likelihood in the CLA procedure slow the rate at which the procedure learns about the population growth rate and survey bias.

High stochastic error in realized bycatch relative to the bycatch limit ($CV=1.0$) sometimes resulted in long-term population status marginally lower than the conservation objective for both the PBR and CLA procedures. Higher stochastic error in survey estimates ($CV=0.6$) resulted in better performance of the management procedures compared to the baseline scenario ($CV=0.2$), while lower error ($CV=0.1$) resulted in worse performance. This effect of survey precision on performance was more pronounced for the CLA procedure than for the PBR procedure (Fig. 4.3). More frequent surveys (every 5 years) also resulted in slightly worse performance of the CLA procedure. It is perhaps counter-intuitive that more precise information about population size resulted in unsatisfactory performance of the management procedures. This occurred because the procedures are by design conservative with respect to the amount of available information about the population. The less information that was available (i.e. fewer, less precise surveys), the lower the bycatch limits and the higher the final population status. Conversely, bycatch limits were higher and final population status was lower when more information was available. When tuning these management procedures it is important to consider what a conservative survey precision and frequency might be, with lower survey precision and higher survey frequency being more conservative. Estimates of abundance for small cetacean populations typically have CVs that are considerably higher than 0.1 and the two surveys that have been conducted for harbour porpoise in my study area were 11 years apart so I considered my tunings to be conservative.

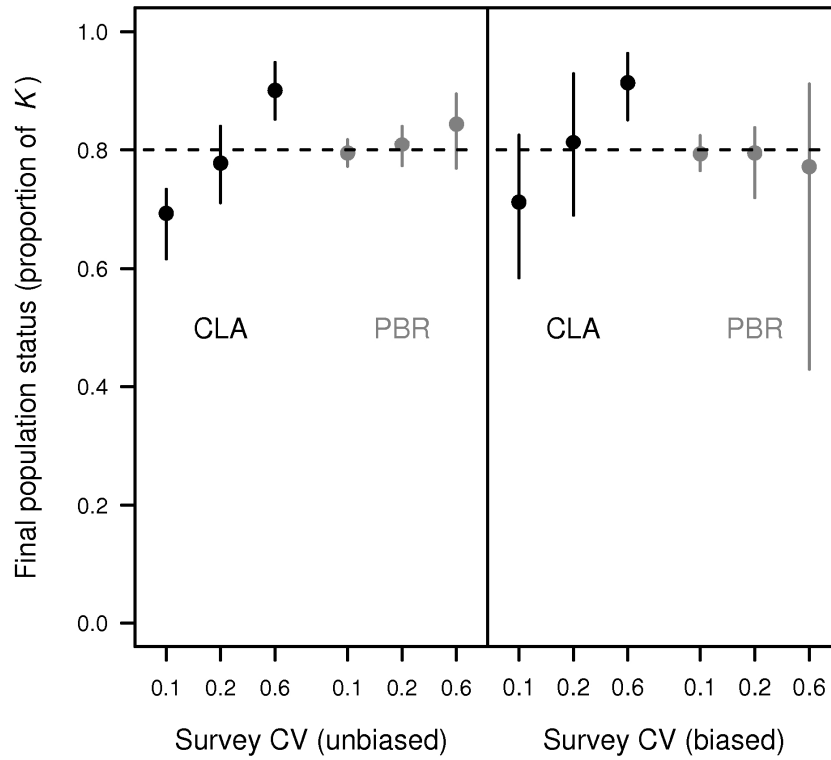


Figure 4.3. Final population status versus survey precision in simulation trials of the first tuning of the PBR and CLA management procedures. Results are shown for unbiased and biased estimates of survey CVs; biased estimates were half the true CV. Initial population status was 0.80 and all other parameters were set to their baseline values (Table 4.1). Points represent median results from 100 simulations and error bars represent the 90% interval of simulation outcomes. The horizontal dashed lines indicate the conservation objective: population status = 0.80.

Bias in estimates of survey precision affected the performance of both management procedures (Fig. 4.3). When estimated survey CVs were high (0.6) and were underestimates of the true CVs (1.2), the performances of the first and second tunings of the PBR procedure were poor. Bycatch limits were highly variable under the PBR procedure when stochastic error in survey estimates was high resulting in highly variable final population statuses. Underestimation of the survey CVs resulted in higher bycatch limits worsening the effect of the high true CV. Median final population status was still close to 80% with the first tuning, but the lower 90% bound of final population status was very low (as low as zero in one case). When the baseline estimated survey CV (0.2) was accurate or was an overestimate of the true CV (0.1) the median final population status was sometimes slightly lower under the first tuning of the CLA than in the baseline scenario where the true survey CV (0.4) was twice the estimated CV. Thus, a decrease in the true variability in survey estimates affected the median performance of the CLA procedure even when the estimate of survey variability did not change.

In simulation trials with environmental variability, bycatch as limited by the management procedures generally did not result in substantially worse population status. In trials where carrying capacity decreased linearly to half its original value over the 200-year simulation period, the conservation objective was achieved under all three tunings of both procedures. In these trials the conservation objective was interpreted as 80% of *final* carrying capacity. In similar trials where carrying capacity increased by 50% over the 200 years, median final population status was always higher than the original carrying capacity, but not always $\geq 80\%$ of the final carrying capacity particularly for the first tuning. Trials with annual stochasticity in birth rate increased the variability in long-term population status and thus resulted in slightly worse performance of the second tuning of the management procedures. This effect was greater when annual deviations in birth rate were assumed to be auto-correlated over time (even though the CV of the deviations themselves was the same for different levels of autocorrelation - Eq. 4.20). Median long-term population status was less affected by this stochasticity so the first tuning performed satisfactorily in these trials, although marginally worse performance occurred with the first tuning of the PBR procedure and auto-correlated deviations. In trials with periodic catastrophic mortality events, the conservation objective was not achieved even with zero bycatch.

Calf abandonment as a result of bycatch resulted in worse performance of the management procedures relative to the baseline scenario although the effect was relatively small. For example, in 1000 simulation trials of the first tuning of the PBR procedure final population status was 0.78 (90% probability interval of 0.70-0.84) with calf abandonment and 0.80 (0.72-0.85) without calf abandonment. Under the first tuning of the CLA procedure final population status was 0.79 (0.65-0.92) and 0.81 (0.67-0.93) with and without calf abandonment, respectively.

Third tuning

With the third tuning of the management procedures, the conservation objective was always achieved when all parameters other than the trial parameter of interest were set at their baseline values (within the ranges of uncertainties considered for the trial parameters). Trials where maximum net productivity was at a population status <0.50 ($z = 0.1$) or where the worst-case values for survey and bycatch estimation bias were combined with a maximum population growth rate of 2% per year resulted in poor performance. Thus, the third tuning is not necessarily conservative for species other than harbour porpoise.

Historical bycatch time-series

In simulation trials where a complete, accurate time-series of historical bycatch estimates was available, short-term recovery of highly depleted populations was faster under the CLA procedure than under the PBR procedure because of an initial period of zero bycatch set by the internal protection mechanism of the CLA procedure, which is absent from the PBR procedure (Fig. 4.2). The median realized protection level (RPL) for highly depleted populations was generally close to 0.5 although there was variability about the median. RPL varied little between the three tunings of the CLA procedure because the internal protection threshold (γ) did not differ between tunings. Median RPL was slightly <0.5 in some cases, for example when abundance was overestimated or when there were frequent surveys. RPL was even lower in trials with catastrophes, $z = 0.1$, maximum population growth rate = 2% and the worst-case scenario.

In trials of the CLA procedure without a time-series of historical bycatch, bycatch limits were always >0 because the CLA assumed that the population was initially at

100% of carrying capacity, regardless of the true depletion. In these trials, the third tuning of the CLA procedure (worst-case scenario) achieved the conservation objective after 200 years for all initial population statuses. However, for the first and second tunings of the CLA procedure depleted populations did not recover sufficiently to meet the conservation objective within 200 years. This was probably because this time period was insufficient for the procedure to reconcile the difference between true initial depletion and the assumed initial depletion.

A feature of this failure was that in some trials of the CLA procedure without a historical bycatch series, the population had clearly not equilibrated in 200 years. This lack of equilibration was most problematic when the population was depleted (Fig. 4.4). The population would initially decrease or remain stable because of a lack of protection and high bycatch limits. Bycatch limits would then decrease and the population would begin to recover but as the population recovered bycatch limits would increase again and the population would begin to decline. In some cases the population had again started to recover by the end of the 200-year simulation period. This behaviour was most pronounced in trials in which abundance was overestimated, bycatch was underestimated, or there were frequent, precise survey estimates. The procedure was simply unable to cope with such severely misleading information. This behaviour was also evident in other trials of the CLA where historical estimates of removals were only half the true removals (Aldrin et al. 2006). Increasing the weighting of the likelihood in the CLA (i.e., increasing w) would theoretically decrease the time that it would take the procedure to correct for misleading information. However, the effect of increasing the likelihood weighting should be similar to the effect of increasing the precision of the abundance estimates so the behaviour described above would still occur.

In practice, in the absence of a historical bycatch series but with knowledge that bycatch has been taken, the conservative approach would be either to choose the third tuning of the CLA procedure, or to choose the first or second tunings but provide the procedure with a conservative historical bycatch series based on the best available information. These considerations are not relevant for the PBR procedure because it does not use bycatch data.

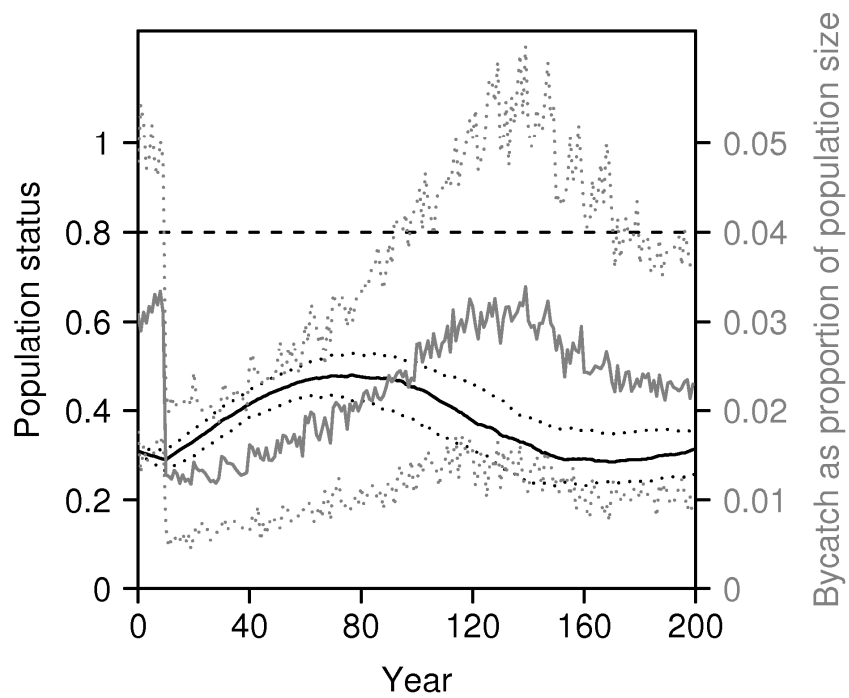


Figure 4.4. Trajectories of population status and bycatch in a simulation trial of the first tuning of the CLA management procedure where no time-series of historical bycatch was input to the procedure. Initial population status was 0.30, survey CVs were 0.10 (unbiased) and all other parameters were set to their baseline values (Table 4.1). Solid lines represent median results from 100 simulations and dotted lines represent the 90% interval of simulation outcomes. The dashed line indicates the conservation objective (population status = 0.80).

Fishery-related performance criteria

In addition to the management procedures' performance with respect to the conservation objective and recovery delay, several fishery-related performance criteria were examined in the simulation trials. Important criteria for fisheries might be total fishing effort and stable fishing effort over time. If it is assumed that bycatch is proportional to fishing effort and the size of the cetacean population then total bycatch limits (as a proportion of population size) are proportional to limits on total fishing effort. Similarly, variability in bycatch limits would translate into variability in limits to fishing effort. The first tuning of the procedures resulted in the highest bycatch limits while the third tuning resulted in the lowest. Bycatch limits were generally more variable over time within simulations under the PBR procedure than under the CLA procedure and this difference increased with the survey CV (Fig. 4.5).

Multi-subpopulation simulations

Managing two hypothetical subpopulations with separate management areas resulted in the conservation objective being achieved for both subpopulations (Figs 4.6 and 4.7). Managing both subpopulations with one management area did not achieve the conservation objective for a subpopulation that was twice as vulnerable to bycatch as the other. However, substantial dispersal between the subpopulations (5% per year) counteracted differential vulnerabilities to bycatch.

Implementation for harbour porpoise in the North Sea

Bycatch limits calculated using the PBR and CLA procedures were <2000 harbour porpoise for the entire North Sea (Table 4.3). Bycatch limits were highest with the PBR procedure for the North Sea as a whole and for the southern sub-area, but were highest with the CLA procedure for the northern sub-area (except the third tuning). The sum of bycatch limits for the northern and southern sub-areas was lower than the bycatch limit calculated for the entire area in all cases. Although the most recent estimate of abundance for the southern sub-area was higher, and its CV lower, than for the northern sub-area, bycatch limits were much lower for the southern sub-area with the CLA procedure. These low bycatch limits likely resulted for two reasons.

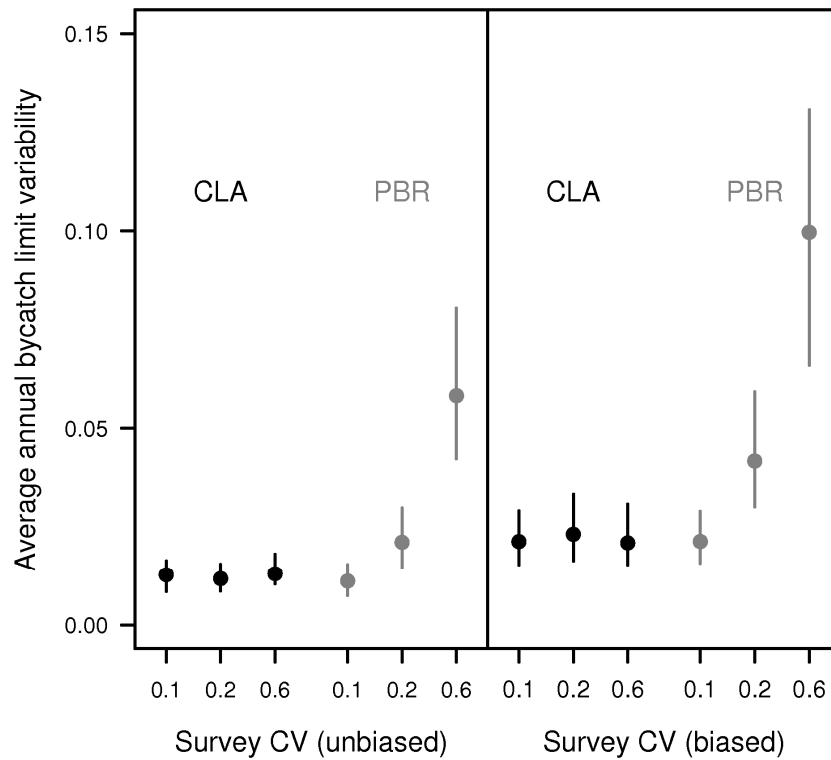


Figure 4.5. Average annual bycatch limit variability versus survey precision in simulation trials of the first tuning of the PBR and CLA management procedures. Results are shown for unbiased and biased estimates of survey CVs; biased estimates were half the true CV. Initial population status was 0.80 and all other parameters were set to their baseline values (Table 4.1). Points represent median results from 100 simulations and error bars represent the 90% interval of simulation outcomes.

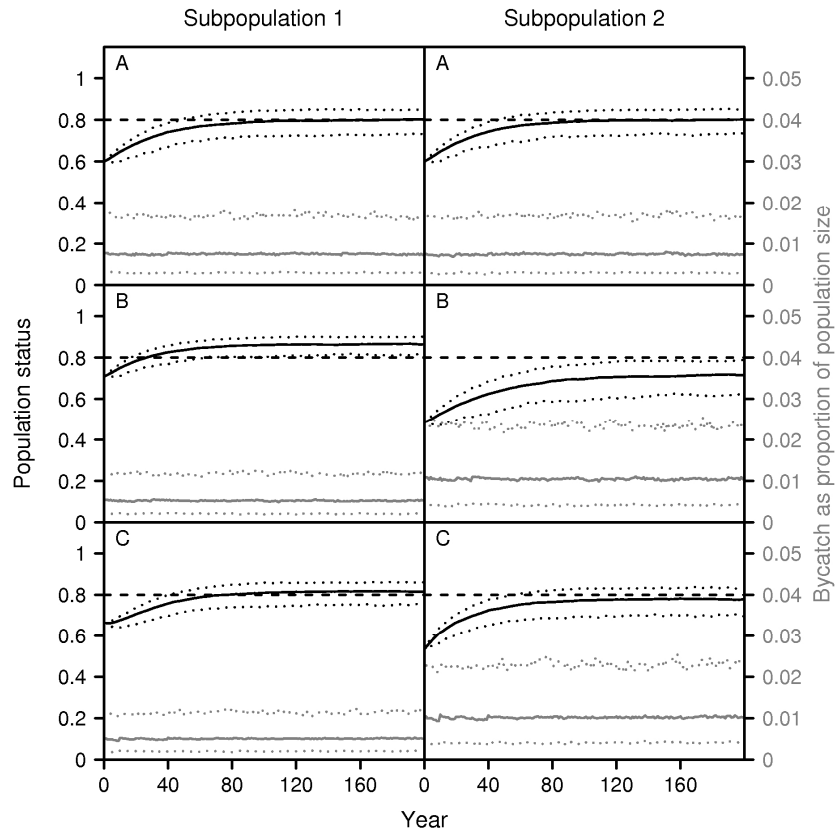


Figure 4.6. Trajectories of population status (population size as proportion of carrying capacity) and bycatch (as proportion of population size) under the first tuning of the PBR procedure in hypothetical multi-subpopulation simulation Scenarios A-C. Solid lines represent median results from 1000 simulations and dotted lines represent the 90% interval of simulation outcomes. The dashed lines indicate the conservation objective (median population status = 0.80). In Scenario A the subpopulations were managed with two separate management areas whose boundaries corresponded to the ranges of the subpopulations. In Scenario B the subpopulations were managed with one management area encompassing the ranges of both subpopulations, but the second subpopulation was twice as vulnerable to bycatch as the first subpopulation. Scenario C was identical to Scenario B with the exception that each subpopulation had a dispersal rate of 5% per year.

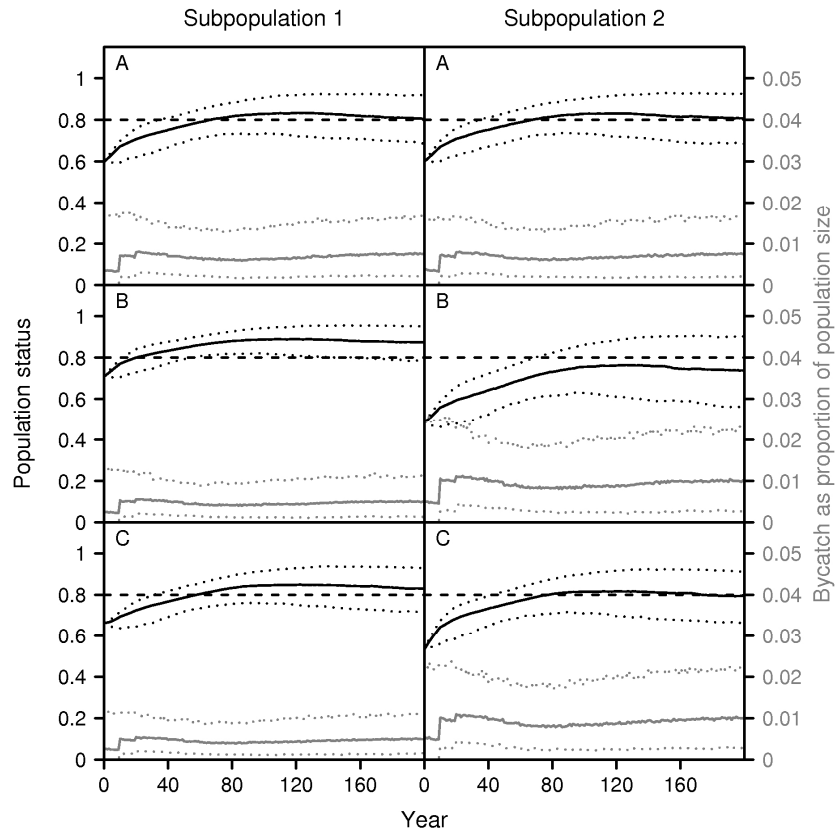


Figure 4.7. Trajectories of population status (population size as proportion of carrying capacity) and bycatch (as proportion of population size) under the first tuning of the CLA procedure in hypothetical multi-subpopulation simulation Scenarios A-C. Solid lines represent median results from 1000 simulations and dotted lines represent the 90% interval of simulation outcomes. Dashed lines indicate the conservation objective (median population status = 0.80). In Scenario A the subpopulations were managed with two separate management areas whose boundaries corresponded to the ranges of the subpopulations. In Scenario B the subpopulations were managed with one management area encompassing the ranges of both subpopulations, but the second subpopulation was twice as vulnerable to bycatch as the first subpopulation. Scenario C was identical to Scenario B with the exception that each subpopulation had a dispersal rate of 5% per year.

Table 4.3. Example bycatch limits for harbour porpoise in the North Sea using the tuned PBR and CLA management procedures. Time-series of historical bycatch input to the CLA management procedure are presented in Table 4.2.

Area	PBR tuning			CLA tuning		
	1	2	3	1	2	3
North Sea	1685	1246	403	1449	840	211
Northern North Sea	698	516	166	1075	623	156
Southern North Sea	964	712	230	216	125	31

First, the total estimated historical bycatch was higher for the southern sub-area so the CLA procedure would have estimated this subpopulation to have been at a lower fraction of its carrying capacity. Second, the abundance estimate for the northern sub-area in 1994 was much higher than for the southern sub-area resulting in a higher average abundance estimate for the northern sub-area. Bycatch limits calculated using the PBR procedure ranged from 0.2% of the point estimates of abundance with the third tuning to 0.8% with the first tuning (Table 4.3). Under the CLA procedure bycatch limits ranged from 0.02-1.2% of the point estimates of abundance.

The performance of all three tunings of the management procedures was poor when the operating model was conditioned on the integrated population dynamics model (Fig. 4.8). Initial population status ranged from about 0.15-0.60. Median population status increased throughout the 200-year simulation period, but median final population status was only ≥ 0.80 under the third tuning. Median final population status was slightly higher under the CLA procedure than under the PBR procedure. The lower bound of the 90% probability interval for population status decreased throughout the simulation period for the first and second tunings of the PBR procedure, but remained relatively constant or increased for the third tuning and for all tunings of the CLA procedure. The 90% probability interval for final population status was very wide in all cases, spanning the majority of the range 0-1. The cause of the poor and highly variable performance of the management procedures was the low median estimate and wide posterior probability interval for maximum population growth rate from the integrated population model (median=1.02, 95% credible interval=1.00-1.07).

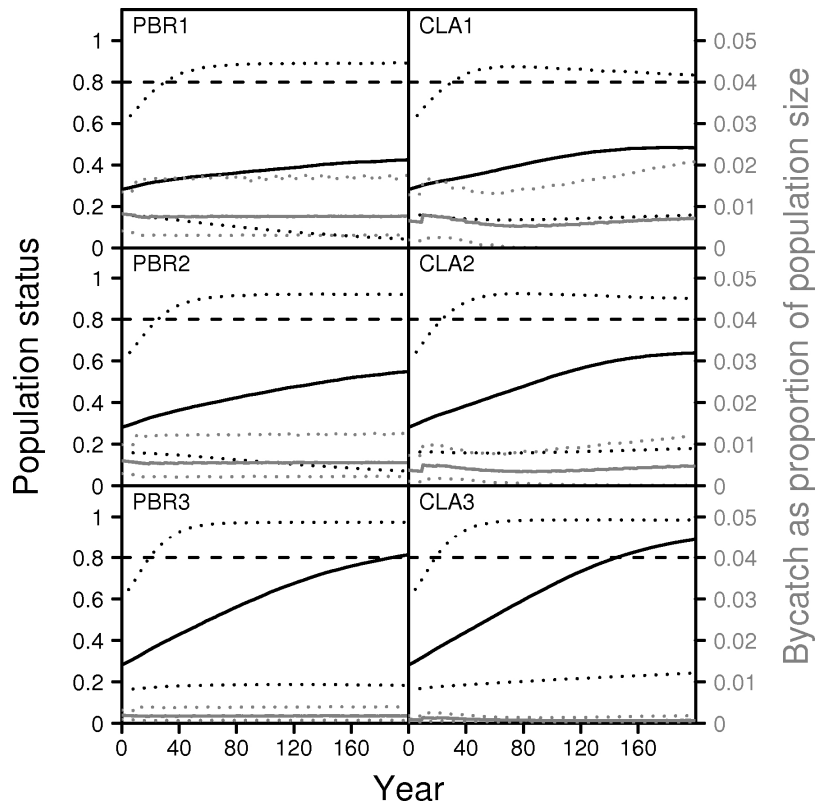


Figure 4.8. Trajectories of population status and bycatch (as proportion of population size) under three tunings of the PBR and CLA management procedures conditioned on the results of the integrated population dynamics model (Chapter 3, Scenario 6). Parameters common to the integrated and operating models were set according to the joint posterior probability distribution; other parameters were set to their baseline values (Table 4.1). Solid lines represent median results from 10,000 simulations and dotted lines represent the 90% interval of simulation outcomes. The dashed line indicates the conservation objective (population status = 0.80).

Discussion

Which procedure?

The PBR and CLA management procedures are both robust mechanisms for setting bycatch limits that can be expected to achieve conservation objectives. However, if a procedure is to be used in the real world then one needs to be chosen. My simulations revealed some key differences between the two procedures. The PBR procedure is an empirical management procedure whose only required input is a single estimate of abundance and its precision. Thus, the PBR procedure is easy to understand and implement. Bycatch limits are approximately a constant proportion of population size so that changes in expected population size are monotonic toward a single equilibrium. However, bycatch limits are sensitive to current estimates of abundance and thus are quite variable over time especially when variability in survey estimates is high. The CLA procedure is a model-based management procedure that makes use of information on previous bycatch and abundance, which allows for a more informed assessment of population status. Thus, the CLA procedure can implement a protection mechanism that allows faster short-term recovery of highly depleted populations. The model-based CLA procedure provides stability and momentum in estimates of population size and status over time so bycatch limits are less sensitive to current estimates of abundance and are less variable over time. However, the inertia provided by the model-based CLA procedure can sometimes result in greater variability in realized performance (i.e., among simulations) and the procedure can perform quite poorly when the input information is highly misleading.

Neither management procedure is clearly better than the other in all cases. Choices between these procedures have to be made on a case-by-case basis. In the case of harbour porpoise in the North Sea, there are estimates of historical bycatch and two estimates of abundance 11 years apart so there is an advantage to using the CLA procedure. Indeed, this was one reason why the joint IWC/ASCOBANS Working Group recommended the development of such a procedure for the harbour porpoise in the North Sea and adjacent waters (IWC 2000). Use of the CLA procedure would specify a zero bycatch limit for a highly depleted population, although, the CLA procedure estimated that the population is not currently highly depleted. Bycatch limits would be more stable over time under the CLA procedure which would make

management actions to implement them easier. Finally, the CLA procedure would learn about the population growth rate over time and would adjust bycatch limits appropriately, albeit slowly. While the PBR procedure is a conservative mechanism for setting bycatch limits in data-poor situations (Hammill and Stenson 2007), I feel that the data available for harbour porpoise in the North Sea make the CLA procedure a more appropriate choice.

Which tuning?

The three tunings developed allow for three interpretations of the conservation objective adopted from ASCOBANS, which is to allow populations to recover to and/or maintain 80% of carrying capacity in the long term. The first tuning of the management procedures is a robust mechanism for setting bycatch limits to achieve a conservation objective of allowing a population to recover to and be maintained *at* 80% of carrying capacity. The second tuning achieves a conservation objective of maintaining a population *at or above* 80% of carrying capacity. Satisfactory performance of the first and second tunings depends on the availability of unbiased data on abundance and bycatch. The third tuning is a highly conservative approach to maintaining a population *at or above* 80% of carrying capacity *in a worst-case situation* where time-series of estimates of abundance and bycatch might be considerably biased upwards and downwards, respectively.

If input data are judged to be of sufficient accuracy then either the first or the second tuning is appropriate. If consistent bias in either abundance or bycatch of the magnitude tested was considered plausible, then the third tuning might be more appropriate. I recommend that for application/implementation for a particular species in a particular region, the judgement of which tuning to use be based on an assessment of the available information. This may include conducting more simulation testing in cases where it is not clear whether or not a procedure is robust to plausible uncertainties. If the third tuning were adopted because of such uncertainty, more information, especially on bycatch, would allow a re-evaluation in the future.

The time-series of historical bycatch that I input to the CLA procedure to calculate bycatch limits for harbour porpoise in the North Sea (Table 4.2) were very likely underestimates of the true historical bycatch (Chapter 3). These time-series did not include estimates of bycatch prior to 1987 or estimates of bycatch in unobserved

fisheries or fisheries of countries other than the UK and Denmark. Unfortunately, it is difficult to say how much the historical bycatch was underestimated. The most conservative approach would be to use the third tuning of the CLA procedure although the first and second tunings might perform adequately if the historical bycatch was not a lot higher than my estimates.

None of the tunings of the PBR and CLA procedures performed well in simulations where the operating model was conditioned using the integrated population dynamics model from Chapter 3. The reason for this was the posterior probability distribution for maximum population growth rate used in conditioning. The median of the posterior for maximum population growth rate was 2%, which is only half the rate that I assumed when tuning the management procedures (4%). In the integrated model a relatively uninformative prior probability distribution was used for maximum population growth rate with a lower bound of zero and a large probability that maximum population growth rate was less than 4% (Chapter 3). The data that the integrated model was fitted to were not informative about maximum population growth rate thus the posterior was similar to the prior. As a result, the posterior distribution for maximum population growth rate is more indicative of the uninformative prior assumption rather than new information about maximum population growth rate provided by the data. Essentially the combination of data and model presented in Chapter 3 did not provide any information about the maximum growth rate of the harbour porpoise population in the North Sea. Thus, the poor performance of the tuned management procedures in the conditioned trials is not a cause for concern. The fact that median trajectories of population status increased under all tunings is actually reassuring given the severe test provided by the conditioned simulations.

Further simulation testing

The PBR and CLA management procedures are generic and could be applied to manage removals from many populations. However, before implementing either management procedure for a given species simulations should be conducted to explore the performance of the procedure over the range of plausible hypotheses about key biological parameters for that species (e.g., maximum population growth rate). The satisfactory performance of my tunings is contingent on my assumptions

about what values were conservative for these parameters. My tunings were designed to be conservative for the management of a harbour porpoise population, but these tunings are not necessarily applicable to other small cetacean species with different life histories.

An important consideration in the application of the management procedures is population structure and spatial management, particularly the correspondence between management areas and subpopulation boundaries. Ideally, management areas for which bycatch limits are set would correspond to the ranges of individual subpopulations, but if population structure is unknown then it would be impossible to ensure this correspondence. As my simulations demonstrated, a danger arises if a bycatch limit is applied to a given management area but animals within that management area are from two or more subpopulations that do not mix freely. If fishing effort (and thus bycatch) is limited to only part of the management area then animals from one or more subpopulations could be more vulnerable to bycatch than animals from other subpopulations within the management area. A bycatch limit based on the total number of animals in the management area would not be appropriate for the smaller number of animals that is actually vulnerable to bycatch.

If population structure is not well understood then a conservative approach to designating management areas is to create the largest management areas within which it is believed that animals definitely mix and interbreed freely (Hammond and Donovan In press). Management areas larger than that size could jeopardize distinct subpopulations within them. The use of smaller management areas confers additional conservation because CVs of survey estimates of abundance in individual areas are often larger than CVs of estimates of total abundance for combinations of these areas. Higher survey CVs result in lower bycatch limits on average under both management procedures.

Ideally, simulation testing should be used to examine the performance of different numbers and arrangements of management areas under different hypotheses about species-specific population structure and movement. Population structure and movement is one of the main focuses of performance-testing simulation trials of the CLA procedure conducted by the IWC for individual species (implementation simulation trials; IWC 2008). The CLA procedure is actually only the core of a larger

management procedure used by the IWC called the Revised Management Procedure (RMP). The default approach under the RMP is to calculate catch limits for individual 'Small Areas' within which animals are considered to mix and interbreed sufficiently. The RMP also allows for several multi-stock rules for calculating and distributing catch limits among management areas including catch-capping and catch-cascading, and the performance of these rules is tested through simulation (Hammond and Donovan In press).

Multiple studies have found significant genetic (Walton 1997, Wang and Berggren 1997, Tolley et al. 1999, Andersen et al. 2001, Tolley et al. 2001, Duke 2003, Thatcher 2005, Tolley and Rosel 2006), phenotypic (Börjesson and Berggren 1997), and ecological (Kleivane et al. 1995, Berrow et al. 1998, Berggren et al. 1999, Tolley and Heldal 2002, Teilmann et al. 2004) differences among harbour porpoises from different areas within the North Sea and European Atlantic. At a region-wide scale there is evidence that patterns of genetic differentiation might be best described as isolation-by-distance (Tolley and Rosel 2006, Fontaine et al. 2007a). Nevertheless, it is difficult to determine whether distinct subpopulations exist and what the boundaries between these subpopulations might be. Taylor and Dizon (1999) caution against using the results of traditional hypothesis tests on genetic data alone to designate management areas. If an isolation-by-distance pattern applies at spatial scales smaller than the entire region, then the designation of subpopulations would simply be a convenient way of delineating the mostly continuous distribution of harbour porpoise across the region. Regardless of the exact population structure, quantitative estimates of dispersal rates of harbour porpoise are not currently available. Given this uncertainty about the spatial dynamics of the harbour porpoise population in the North Sea, it is difficult to formulate appropriate scenarios for simulation testing and to designate management areas. In the interim, the separate bycatch limits calculated for the northern and southern sub-areas are more conservative than the bycatch limits calculated for the North Sea as a whole (Table 4.3).

In addition to population structure there are at least three other important considerations for future simulation testing: other factors influencing population dynamics, indirect effects of bycatch on the population, and indirect effects of bycatch on the ecosystem (Milner-Gulland 2008). Bycatch is only one of a suite of ecological

and anthropogenic factors affecting the dynamics of harbour porpoise populations. For example, bottlenose dolphin attacks have been identified as a major source of mortality in some parts of the UK and the frequency of these attacks might have increased in recent years (Ross and Wilson 1996, Jepson 2003). Anthropogenic chemical pollutants have been demonstrated to increase the risk of infectious disease in harbour porpoise (Hall et al. 2006). Bycatch mortality was the only specific source of mortality that I considered in my simulations; other mortality was accounted for through 'natural' survival rates. Furthermore, carrying capacity represented the population size that would be reached in the absence of bycatch, which is not necessarily the natural carrying capacity. To achieve the conservation objective in terms of natural carrying capacity the removal limits calculated by the management procedures should be considered as limits to total anthropogenic mortality rather than limits to bycatch. If quantitative estimates of other ecological and anthropogenic mortalities are available these should be included in performance-testing simulations.

Removals from wild populations can have effects beyond the simple direct reduction in the number of animals in the population (Hilborn et al. 1995). For example, I considered the effect that bycatch of lactating females might have on their dependent young. Mating systems and complex social structures can be vulnerable to the removal of particular types of individuals and the breakdown of those structures can result in increased mortality and decreased reproduction (Stephens et al. 2002, Milner-Gulland et al. 2003, Williams and Lusseau 2006, Milner et al. 2007). Ultimately, selective removals can have evolutionary effects on populations (Law 2000, Proaktor et al. 2007). Habitat degradation is another potential indirect effect of bycatch if surviving animals avoid areas where they encountered fishing nets previously. If indirect effects of removals on mortality and reproduction can be quantified then these effects should be incorporated in future simulation testing.

Multi-species and ecosystem models would provide the most realistic operating models for testing the performance of management procedures (Marasco et al. 2007). Ecosystem models have demonstrated that even sustainable removals of one species can have large and sometimes unexpected effects on the abundance of other species (Yodzis 1998, Walters et al. 2005). At least one study has considered the performance of the CLA procedure for setting catch limits for minke whales in a multi-species

context (Schweder et al. 1998). The complexity added by multi-species and ecosystem modelling is a major challenge for the MSE approach.

Extensions to the management procedures

I considered two existing management procedures for my purposes, an empirical procedure and a model-based procedure. There are several possible extensions to these management procedures. One extension of the CLA management procedure that could prove useful is the addition of data on relative abundance. The algorithm could easily accommodate relative abundance data through the addition of a parameter that scales relative abundance to absolute abundance. The most efficient method might be to integrate this parameter out of the likelihood or set it to its maximum likelihood value (Walters and Ludwig 1994, Cooke 1999). Covariance between estimates of absolute abundance and relative abundance could also be incorporated (Cooke 1999, McDonald et al. 2001). The IWC explored the use of catch-per-unit-effort data as indices of relative abundance early in the development of the CLA procedure, but it was decided that the difficulties associated with catch-per-unit-effort data diminished their usefulness (Hammond and Donovan In press). The major difficulty in using catch-per-unit-effort data is that the proportional relationship between catch per unit effort and absolute abundance is rarely constant (Harley et al. 2001, Maunder et al. 2006). Nevertheless, standardised indices of abundance from scientific surveys, such as those presented in Chapter 2, could provide useful information to a model-based procedure like the CLA. Simulation testing could be used to examine how useful these data might be.

An alternative management procedure that might be useful is a procedure that calculates a fishing effort limit. The PBR and CLA management procedures provide bycatch limits. These limits are only directly useful to a management framework with output controls, for example, the use of individual transferable bycatch quotas (Bisack and Sutinen 2006) or a framework where the fishery is closed if the limit is reached (Maunder et al. 2000). Bycatch limits are not directly useful to a management framework with input controls (i.e., controls on fishing effort like time/area closures). To achieve a bycatch limit by managing fishing effort, one must know or have an estimate of the relationship between bycatch and fishing effort. Most previous management procedures have been focused on output controls, but procedures

focused on input controls have been considered (Punt and Donovan 2007, Hoff and Frost 2008, Kai and Shirakihara 2008). A model-based management procedure with data and a population model similar to those presented in Chapter 3 could theoretically take data on abundance, previous fishing effort and previous bycatch per unit effort and estimate bycatch per unit effort per porpoise abundance. The removal control rule could then be parameterized to give a fishing effort limit. Such a procedure would be sensitive to assumptions about the relationship between bycatch and fishing effort so these assumptions should be tested through simulation.

Implementation

The bycatch limits that I present for harbour porpoise in the North Sea are preliminary. It is important to recognise that these bycatch limits are entirely dependent on the stated conservation objective, on the tunings (and their precision) that were used to achieve it under different interpretations of the conservation objective, and on the data that were input to the procedures. The bycatch limits are therefore indicative and should not be used for management purposes. Several steps need to be taken before a management procedure is successfully implemented for any species in any region. First, policy makers must agree on the exact conservation/management objective(s). Second, scientists must decide whether further simulation testing is necessary including consideration of population structure, spatial design of management and quality and availability of data. Third, policy makers must agree to implement the management procedure and commit to the regular collection of data on bycatch and abundance in the future to feed back into the management procedure. The management procedures developed here are robust, fully-tested mechanisms for determining bycatch limits that will achieve conservation objectives in the long-term. The agreement and commitment of policy-makers, scientists and stakeholders to follow these procedures and adhere to these bycatch limits over time is critical for success.

Chapter 5: General Discussion

Thesis summary

In this thesis I developed methods for determining the impact of bycatch on the state and dynamics of harbour porpoise populations and for calculating bycatch limits to achieve specific and quantitative conservation objectives. I applied these methods to determine the impact of historical bycatch on the harbour porpoise population in the North Sea and to calculate preliminary bycatch limits for the North Sea.

Monitoring trends in abundance is the most direct method of assessing the conservation status of a population subject to bycatch. There are only two estimates of harbour porpoise abundance for the European Atlantic and North Sea 11 years apart. However, there are more data available on relative abundance (e.g., sighting rates) that could potentially improve estimates of population trend. Some of the most numerous data on harbour porpoise sightings with the widest geographic coverage are those collected on European Seabirds at Sea (ESAS) surveys. In Chapter 2, I analysed sighting rates of porpoise on ESAS surveys in the North Sea during 1980-2003 to determine whether these data could provide informative time-series of relative abundance. Generalized additive models were used to standardise sighting rates by controlling for other variables that affected the sightability and abundance of harbour porpoise. Some general estimated patterns and trends in harbour porpoise sighting rates were consistent with previous studies. For example, there was a general increase in sighting rates from the late 1990s onward in two areas of the southern North Sea and a decrease in the western North Sea from the late 1990s onward. However, sighting rates were low overall and the standardised annual indices of abundance had relatively low precision (CVs ranged from 0.32-2.5). Thus, the derived time-series of relative abundance have limited value for a population monitoring framework that relies on the statistical detection of population trend. For example, survey estimates every two years with CVs of 0.32 would only provide a statistical power of 0.47 to detect an exponential decline of 5% per year over 15 years. Confounding observer and year effects further complicated interpretation of temporal trends. Nevertheless, time-series of relative abundance derived from the ESAS database may enhance integrated analyses of the dynamics of harbour porpoise populations in this region.

In addition to data on abundance, there are other types of data available on harbour porpoise and bycatch in the European Atlantic and North Sea including life history, fishing effort and rates of bycatch per unit fishing effort. In the past these datasets have mainly been analysed separately. The best way to assess the impact of bycatch on the state and dynamics of porpoise populations is to combine all of the available information through an integrated population dynamics model. In Chapter 3, I developed such a model to integrate the available data and assess the population dynamics and conservation status of harbour porpoise in the North Sea during 1987-2005. I was primarily interested in estimating bycatch, population growth rate (with and without bycatch) and carrying capacity. The model was fitted simultaneously to data on abundance and data from the UK and Denmark on age at sexual maturity, pregnancy rate, age at death, and bycatch per unit fishing effort with data on total fishing effort as input. The model was fitted in a Bayesian statistical framework to explicitly account for uncertainty in parameter estimates. Several qualitatively different scenarios were considered with respect to population dynamics (e.g., density-independent or density-dependent birth rate), population structure (one population or two subpopulations) and the data used to fit the model. Median estimates of bycatch were higher than previous estimates, but were also highly uncertain (e.g., mean CV=0.25 for estimates of total bycatch in the base scenario). There was a high probability that this estimated bycatch resulted in a decrease in the number of harbour porpoise in the North Sea during the study period, particularly during the late 1980s and 1990s (e.g., median change of -49% from 1987-2005 with 95% probability interval of -75% to -2% in base scenario; -31%, -53 to 21% in density-dependent scenario). Median estimated population growth rate in the absence of bycatch was close to 0 in density-independent scenarios (e.g., -1, -5 to 3% per year in base scenario). The estimated life history parameters suggested a limited scope for population growth. The model overestimated birth and survival rates highlighting an inconsistency between the observed pregnancy rate and the observed age structure of natural mortality. The density-dependent model and data were not informative about the maximum rate at which the population could grow at low density or the number of harbour porpoise that could be supported in the area. Scenarios with northern and southern subpopulations suggested that dispersal from the north to the south was necessary to produce observed changes in point estimates of abundance between 1994

and 2005 in July. The alternative hypothesis considered—different *in situ* growth rates for the two subpopulations—was not consistent with the data.

While the integrated population dynamics model provided estimates of parameters and variables that are key to management including bycatch and population growth rate, there were still large uncertainties about key quantities. The model and data were not informative about the maximum rate at which the population could grow at low density or the number of harbour porpoise that could be supported in the area. In addition to these uncertainties, inconsistencies between some of the data (e.g., pregnancy rate and age distribution of mortality) highlight the potential for this type of analysis to produce misleading conclusions. Thus, integrated population dynamics modelling alone is insufficient as a framework for managing the bycatch of harbour porpoise.

As identified by a joint International Whaling Commission (IWC)/Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS) scientific working group, there is a need for a robust management procedure that can be used to calculate limits to the bycatch of harbour porpoise that will achieve conservation objectives in the face of uncertainty. In Chapter 4, I considered two candidate management procedures for this purpose: the Potential Biological Removal (PBR) procedure used by the USA Government and the Catch Limit Algorithm (CLA) procedure used by the IWC. I used a simulation-based approach (management strategy evaluation) to compare and contrast the behaviour of the two procedures, to tune the procedures to specific conservation objectives and to test the robustness of the tuned procedures to a wide range of biases, stochasticity and uncertainty with respect to population dynamics and structure, the environment, observation and implementation. Bycatch limits were more variable over time within simulations under the PBR procedure than under the CLA procedure, especially when there were large random errors in estimates of abundance. However, final population status was sometimes more variable across simulations under the CLA procedure. Less precise abundance estimates resulted in more conservative bycatch limits under both procedures, but this effect was more pronounced for the CLA procedure. Short-term recovery of a highly depleted population was faster under the CLA procedure because of its internal protection mechanism. However, the CLA procedure performed poorly

when a population was depleted and this information was not available to the procedure (i.e., no time-series of historical bycatch). I developed three tunings of the procedures based on three specific interpretations of the general conservation objective of ASCOBANS, which is to allow populations to recover to and/or maintain 80% of carrying capacity in the long term. The simulation trials revealed scenarios that could result in unsatisfactory performance of the less-conservative first and second tunings: systematic overestimation of abundance, and systematic underestimation of bycatch. By design, the third tuning performed satisfactorily under what I deemed to be a worst-case scenario. None of the tunings of either procedure performed well in simulations conditioned on the results of the integrated population dynamics model (Chapter 3) because of the extremely large uncertainties associated with the estimates of maximum population growth rate from the integrated model. Nevertheless, median population status increased over time in the conditioned simulations under all tunings of both procedures. Preliminary annual bycatch limits for harbour porpoise in the North Sea ranged from 195-1685 depending on the procedure, tuning and management areas used.

Given that estimates of bycatch and abundance are available for harbour porpoise in the North Sea, the IWC's Catch Limit Algorithm, as tuned in Chapter 4, provides a robust mechanism for calculating limits to bycatch that will achieve the defined conservation objective of maintaining or restoring European populations of harbour porpoise to 80% of carrying capacity.

Achieving bycatch limits

In my baseline population assessment of harbour porpoise in the North Sea (Chapter 3, Scenario 1) the estimated annual bycatch between 1987 and 2005 exceeded the current bycatch limits calculated using the management procedures (Chapter 4). This finding reinforces the need to implement management actions to reduce the bycatch of harbour porpoise in the North Sea. There are two types of management actions that can be taken to reduce bycatch (Hall et al. 2000). The first type of action is to reduce fishing effort (i.e., reduce exposure to hazard; Harwood 1999). The second type of action is to reduce the rate of bycatch per unit fishing effort by reducing the probability of entanglement when harbour porpoise encounter fishing nets (i.e., alter response to exposure; Harwood 1999).

The most effective method for reducing bycatch would be to eliminate fishing effort in areas with harbour porpoise (Dawson 1991). However, the wide geographic ranges of harbour porpoise populations make it impractical to exclude fisheries from these entire areas. Alternatively, fishery closures in specific areas or at certain times of the year may be useful for reducing bycatch. Time/area closures can be effective when bycatch is predictable and limited to a small subset of the area fished (Murray et al. 2000). Unfortunately, harbour porpoise bycatch is generally unpredictable and is not limited to a small subset of the area fished. For example, a month-long time/area closure in the Gulf of Maine sink gillnet fishery resulted in simple displacement of fishing effort to adjacent areas where bycatch of harbour porpoise still occurred (Murray et al. 2000). Nevertheless, there is evidence of seasonal variability in bycatch rates (Vinther and Larsen 2004) and seasonal movements of harbour porpoise in the North Sea and adjacent waters (Andersen 1982, Camphuysen 2004, Siebert et al. 2006) so it may be possible to reduce bycatch by reducing fishing effort in seasons and areas with relatively higher bycatch rates and higher harbour porpoise densities. Another option is dynamic time/area closures whereby closures are triggered by real-time observations of animal density or bycatch, such as those used to mitigate bycatch of North Atlantic right whales off the east coast of the USA (Clapham and Pace 2001). However, dynamic closures require a high level of monitoring effort which is unlikely to be achieved for harbour porpoise and fisheries in which they are bycaught.

In addition to reducing fishing effort, bycatch can be reduced through modifications to fishing techniques that reduce the rate of bycatch per unit fishing effort. A wide range of fishing techniques have been tried to reduce the bycatch of non-target marine wildlife (Werner et al. 2006). Techniques for reducing harbour porpoise bycatch rates have generally involved technological modifications to gillnet material and the use of acoustic devices. Nets impregnated with different materials such as iron oxide and barium sulphate have resulted in significantly lower rates of bycatch of harbour porpoise (Trippel et al. 2003, Larsen et al. 2007). It is unclear whether the reduced bycatch with these modified nets is because of increased acoustic detection of the modified net material by harbour porpoise or increased stiffness of the modified net material resulting in a lower probability of entanglement. Larsen et al. (2007) found that acoustic target strengths were similar between nets with iron oxide and control nets and suggested that increased stiffness caused the decrease in bycatch. Trippel et

al. (2003) recommended further research to elucidate the mechanism by which barium sulphate in net material reduced bycatch. Koschinski et al. (2006) found that nets with barium sulphate had a higher acoustic target strength and that the acoustic behaviour of wild harbour porpoise was different around these nets compared to control nets. Northridge et al. (2003) actually found higher rates of bycatch of harbour porpoise in nets with barium sulphate in an experimental trial but the control nets had a larger mesh size and a thinner twine diameter. In a separate experimental trial, Northridge et al. (2003) found that nets with thinner twine diameters had a lower rate of bycatch. A potential disadvantage of modified net material is lower catches of target species. Trippel et al. (2003) did not find significantly different catches of commercial fish species in nets with barium sulphate. Larsen et al. (2007) found reduced catch rates of cod but not of three other fish species in nets with iron-oxide. Although modifications to net material have not eliminated bycatch altogether, the evidence suggests that they are useful for reducing the rate of bycatch of porpoise while maintaining the catch of target species.

Acoustic devices have also been demonstrated to reduce the rate of bycatch of harbour porpoise. Field experiments have found that the attachment of acoustic alarms to gillnets resulted in fewer bycaught porpoise per unit effort compared to control nets without alarms (Lien et al. 1995, Kraus et al. 1997, Trippel et al. 1999, Gearin et al. 2000, Palka et al. 2008). Acoustic alarms have been used in Danish North Sea gillnet fisheries and observations have indicated a substantially reduced rate of bycatch with alarmed nets (Larsen 1999, Larsen et al. 2002). Studies of the behaviour of wild and captive harbour porpoise have indicated increased average distances from and avoidance of nets and areas with active acoustic alarms and other acoustic harassment devices (Kastelein et al. 2000, Culik et al. 2001, Johnston 2002, Olesiuk et al. 2002). It is not clear exactly why acoustic alarms elicit this response from porpoise. Three possible explanations are that the sounds are aversive, the sounds elicit echolocation and thus increase the probability of detection of the net, or the porpoises learn to associate the sounds with the danger of entanglement (Dawson et al. 1998). It is also possible that the effect of acoustic alarms on harbour porpoise behaviour is indirect. Kraus et al. (1997) found lower catches of herring, one of the main prey of harbour porpoise, in gillnets equipped with acoustic alarms. Porpoises might have been less inclined to interact with nets with fewer herring.

Despite the apparent effectiveness of acoustic alarms for reducing the bycatch of harbour porpoise (although see Dawson et al. 1998), there are several potential disadvantages to their use (Woodley 1995). First, the use of acoustic alarms might exclude harbour porpoise from areas important for foraging, breeding, etc. Second, the use of acoustic alarms might decrease the catch of fish if fish are able to hear the alarm and avoid the nets. As mentioned, Kraus et al. (1997) found lower catches of herring in alarmed nets although catches of the target species cod and pollock *Pollachius virens* were not significantly different from control nets. Other studies have found no significant difference in catches of target species, including herring, between alarmed nets and control nets (Trippel et al. 1999, Gearin et al. 2000, Culik et al. 2001). A third potential problem with acoustic alarms is the alerting of other predators (e.g., seals) to the nets, although two studies found no significant differences in seal depredation or net damage between alarmed and control nets (Kraus et al. 1997, Gearin et al. 2000). Fourth, acoustic alarms might lose their effectiveness over time if animals habituate to them. Cox et al. (2001) reported the results of a field experiment where harbour porpoise appeared to habituate to an acoustic alarm in a matter of days. In general, the use of acoustic alarms will require monitoring and maintenance to ensure their proper functioning over time. Palka et al. (2008) found that gillnets with fewer than the required number of functioning acoustic alarms had more harbour porpoise bycatch than nets without alarms. Noise pollution and chemical pollution from lost or discarded batteries and devices are final disadvantages of acoustic alarms (Woodley 1995).

The main management action that has been legislated by the European Union (EU) to reduce harbour porpoise bycatch in the North Sea is the required use of acoustic deterrent devices “in areas and fisheries with known or foreseeable high levels of bycatch of small cetaceans” (Council of the European Union 2004). The EU has also imposed a ban on driftnet fishing in the Baltic Sea (Council of the European Union 2004). Despite the legislation, the use of acoustic alarms is far from ubiquitous with only limited enforcement (ICES 2008). However, acoustic alarms have been used in some North Sea fisheries such as Danish gillnet fisheries (Larsen 1999, Larsen et al. 2002). Observations suggest that these acoustic alarms can reduce the bycatch of harbour porpoise substantially, but further monitoring is required to evaluate the generality of these findings and the long-term effectiveness of the acoustic alarms. As

demonstrated in Scenario 5 of my population assessment (Chapter 3), if bycatch rates have been reduced in recent years by the use of acoustic alarms (e.g., by 50%) then bycatch could be approaching levels below the bycatch limits. However, bycatch in fisheries of countries other than the UK and Denmark must also be taken into account. Continued monitoring of harbour porpoise bycatch in all relevant North Sea fisheries is essential to determine current and future levels of bycatch.

The human side of the equation

It would be naïve to assume that the development of a management procedure for calculating bycatch limits is a complete solution for ensuring sustainable bycatch. At a minimum, required information about the population must continue to be collected periodically followed by the calculation of new bycatch limits using the management procedure, and most importantly, the bycatch limit must not be exceeded. Changes in conservation objectives are easily dealt with by re-tuning the management procedures, and my simulations suggest that the management procedures can tolerate some bias and error in the observation and implementation processes. However, there are more systematic issues that I did not consider in the simulations.

The human aspect of the system is perhaps the most important factor that I did not model explicitly. History shows that humans have a poor record with respect to sustainable exploitation of natural resources (Ludwig et al. 1993). The management procedures presented here would theoretically minimize the effect of some of the causes of historical failures (e.g., natural variability), but they do not address human behaviour. Hilborn (1995) suggested that “Perhaps the biggest failure in natural resource management has been the widespread neglect of the dynamics of the exploiters”. Fisheries are a human enterprise with great social and economic value. Wealth generates social and political power and can result in unsustainable practices even when biological understanding of the system is relatively good (Ludwig et al. 1993). Furthermore, the sustainability of bycatch is not necessarily related to the sustainability of the fisheries themselves; fisheries that are sustainable with respect to target species can have unsustainable levels of bycatch.

Management actions to achieve bycatch limits will have socioeconomic costs. For example, the deployment of acoustic alarms would incur a direct cost for the

equipment and enforcement (ICES 2008). Reductions in fishing effort and catch would have more widespread implications. These socioeconomic costs would result in a resistance to adhere to the bycatch limits. At worst the limits would be ignored by policymakers and managers, but there could also be compromise, for example where bycatch limits are phased in over time. European legislation related to the bycatch of harbour porpoise explicitly acknowledges socioeconomic considerations. The European Community Habitats Directive states that “measures taken pursuant to this Directive shall take account of economic, social and cultural requirements and regional and local characteristics” (Council of the European Communities 1992). Any complete risk assessment or management framework should consider socioeconomic factors (Harwood 2000, Baxter et al. 2006, Hoydal 2007).

The potential impacts of bycatch limits and resulting management actions on the socioeconomic benefits derived from the fisheries were beyond the scope of the research covered by this thesis. However, the management strategy evaluation (MSE) framework used here could be expanded to consider the dynamics and value of the fisheries, to re-tune the procedures to achieve a specific balance between socioeconomic and conservation objectives, and to explore management policies other than strict adherence to the specified bycatch limits (Milner-Gulland et al. 2004, Pestes et al. 2008). Breen et al. (2003) used a MSE framework to examine the cost of different strategies for managing the bycatch of sea lions to a New Zealand squid fishery. Bioeconomic models integrate the biological and human components of the system and have been used to examine the sustainability of management of removals from populations (Clark 2006, Ling and Milner-Gulland 2006, 2008, van Kooten 2008). Bisack and Sutinen (2006) developed a bioeconomic simulation model to examine the relative costliness of alternative strategies for implementing harbour porpoise bycatch limits to the New England sink gillnet fishery. Their results suggested that an Individual Transferable Quota (ITQ) system was less costly than fisheries closures.

The management procedures and any related management actions to reduce bycatch will also entail economic costs through monitoring and enforcement. For bycatch limits to remain appropriate they must be updated over time by inputting new information on population size and bycatch to the management procedures. Fisheries

must be monitored to ensure that bycatch limits are not being exceeded and that they are complying with management regulations (e.g., use of acoustic alarms). There are trade-offs between the cost of monitoring and the quality and quantity of information provided to the management procedure. More frequent and more precise estimates will cost more to obtain, but better information will also result in more appropriate and possibly higher bycatch limits (Hammond and Donovan In press). Statistical power analyses and simulations can be used to determine types and levels of monitoring that will result in the desired information, accuracy and precision (Northridge and Thomas 2003, Katzner et al. 2007). For example, the Small Cetaceans of the European Atlantic and North Sea - II project (SCANS-II 2008) examined trade-offs between the financial costs, logistical constraints and precision of several survey methods for monitoring harbour porpoise abundance in European waters (passive acoustic and aerial and ship-based visual surveys). Simulation can be used to examine trade-offs between the cost of monitoring and the benefits obtained from the information provided by that monitoring (Hauser et al. 2006). The MSE framework allows one to explicitly evaluate the costs and benefits of a monitoring programme that provides information directly to a management procedure.

A final socioeconomic consideration is the distribution of the costs of management actions among fisheries within and among nations. In the North Sea harbour porpoise are bycaught in a range of fisheries from a number of countries. The bycatch limits specified by the management procedures apply to all of the fisheries combined. It will be a major challenge to develop multi-fishery management actions to achieve an overall bycatch limit. For example, which fisheries should be subject to management actions such as time-area closures? Should this decision be based on observed bycatch or bycatch rates in different fisheries or should it be based on the socioeconomic value of the fisheries? Politics will play a large role in these decisions especially at the international level. The USA Government allocates removal limits from trans-boundary populations of marine mammals according to the proportion of the population residing in USA waters (non-migratory species) and the proportion of time that the population spends in USA waters (migratory species; National Marine Fisheries Service 2005). This issue is especially complex in Europe because of the number of countries and overlap between nations and fisheries (ICES 2008). An ITQ system is one option for allocating bycatch limits among fisheries. Porpoise quotas

could be bought and sold among fisheries with the price dictated by economic forces. The bioeconomic model of Bisack and Sutinen (2006) suggested that an ITQ system for managing harbour porpoise bycatch would result in a better distribution of costs among sink gillnet fisheries in New England than would a system of time-area closures. A bycatch quota system whereby fishing is stopped once a quota had been exceeded (e.g., sea lion bycatch in New Zealand squid fishery; Breen et al. 2003) would require substantial monitoring and enforcement efforts.

Final remarks

The work presented in this thesis is an important and critical step in the process of understanding the impacts of bycatch on harbour porpoise populations in European waters and managing future bycatch to conserve these populations. The methods developed also have broader applicability to other species of small cetaceans and marine wildlife that are subject to anthropogenic mortality. I feel that the management procedure approach presented in this thesis should be adopted as part of the overall strategy for managing the bycatch of harbour porpoise and other small cetaceans in European waters. With regular information on abundance and bycatch a management procedure will specify bycatch limits that are expected to achieve conservation objectives in the long term. The immediate next step is the acceptance and adoption of the management procedure approach and the specification of conservation objectives by policymakers, managers and other stakeholders. Uptake of the approach will require effective communication on the part of scientists so that the approach is understood by groups less familiar with the technical details (Peterman 2004, Pastoors et al. 2007, Reed 2008). There will be many further management challenges, the greatest of which will be designing management actions to achieve bycatch limits while minimising socioeconomic costs. Nevertheless, I am optimistic that these challenges can be met with a robust framework for specifying bycatch limits as a foundation.

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Appendix

Results of performance-testing simulations (Chapter 4)

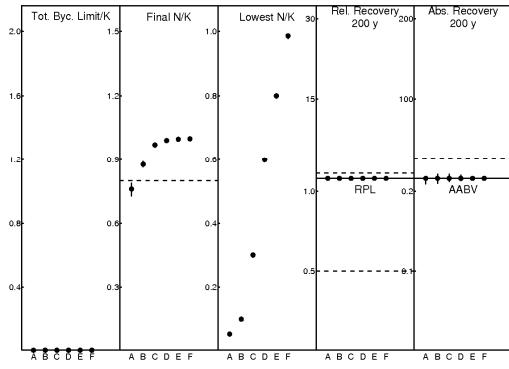
The following series of figures illustrate the results of the generic performance-testing simulations for the three tunings of the management procedures. Each figure represents the outcome of a series of simulation trials for:

- a given management procedure and a given tuning indicated in the x-axis label by PBR or CLA (or 'NoByc' for a simulation without bycatch) and 1, 2 or 3
- a given set of trials with respect to the presence or absence of a historical bycatch series indicated in the x-axis label by 'IWCDep' (set 1 described in Table 4.1; complete historical bycatch series) or 'InitDep' (set 2 in Table 4.1; no historical bycatch series); note that the results of InitDep trials are only presented for the CLA procedure as the PBR procedure does not make use of estimates of historical bycatch
- a range of initial population statuses indicated on the x-axis by letters A-E representing 0.05, 0.10, 0.30, 0.60, 0.80, and 0.99/1.00 of carrying capacity, respectively (Table 4.1)
- a given maximum population growth rate indicated in the x-axis label by 'rmax'
- a given value for the bottom-level trial parameter of interest (Table 4.1) indicated in the x-axis label; Table A.1 lists the label that corresponds to each parameter

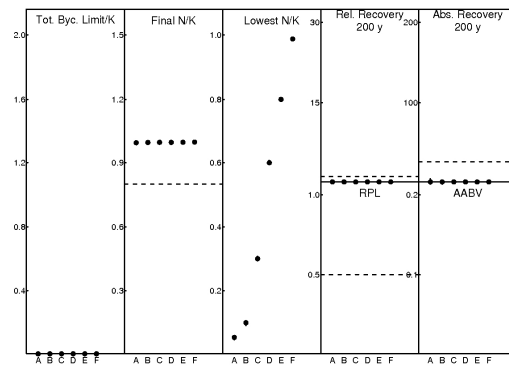
Each figure is composed of seven panels representing the seven performance metrics described in Chapter 4 (Eqs 4.25-4.33). For each performance metric, the results of 100 simulations for each trial are summarized by the median outcome (filled circle) and 90% interval of outcomes (vertical error bars). Black circles and error bars indicate that the median final population status was greater than or equal to the median initial population status, while red symbols indicate a decline in median population status over the simulation period. Missing circles or error bars in the Abs. Recovery and Rel. Recovery panels indicate that the median or 90% interval population status did not recover to the target during the simulation period. Note that this does not necessarily mean that the population would have recovered to 80% of carrying capacity in the absence of bycatch. The horizontal dashed line in the Final N/K panels indicates the conservation objective—80% of carrying capacity. For trials with changes in carrying capacity (KChange), this line represents 80% of final carrying capacity. The horizontal dashed line in the RPL panels indicates the fixed protection level internal to the CLA procedure— $\gamma=0.5$. The horizontal dashed line in the Abs. Recovery panels indicates 25 years. The horizontal dashed line in the Rel. Recovery panels indicates 1—a 100% delay in recovery (i.e., recovery takes twice as long).

Table A.1. Labels corresponding to parameters (Table 4.1) in figures.

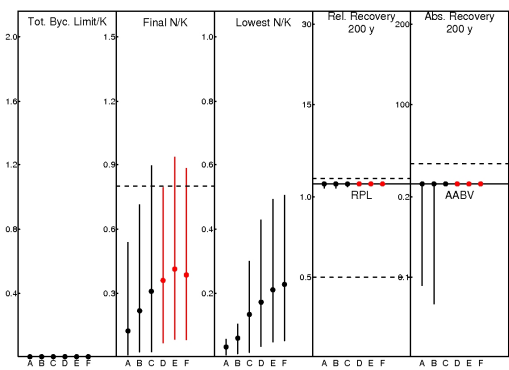
Parameter(s)	Label
All parameters at tuning values	Tune
All parameters at baseline values	Base
Shape of density dependence (z)	z
Survey bias (B^0)	BiasSrvyAbs
Survey precision (CV^0)	SrvyCVAbs
Survey precision unbiased (CV^0 ; $B^{CV^0}=1$)	SrvyCVAbsUnbias
Survey CV bias (B^{CV^0})	BiasSrvyCVAbs
Bycatch bias (B^{byc} ; does not apply to historical bycatch)	BiasByc
Bycatch precision (CV^{byc} ; does not apply to historical bycatch)	BycCV
Survey frequency (f)	SrvyFreq
Change in carrying capacity ($\sum_{a=0}^{\omega} N_a^K$)	KChange
Catastrophic natural mortality events ($P^{catastrophe}=0.02$)	Cat
Environmental stochasticity autocorrelation (φ ; $CV^{env}=0.2$)	EnvStoch20AC



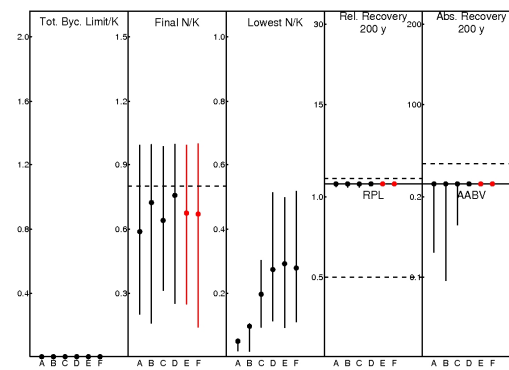
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (NoBycIWCDep, Base = 1, rmax = 2%)



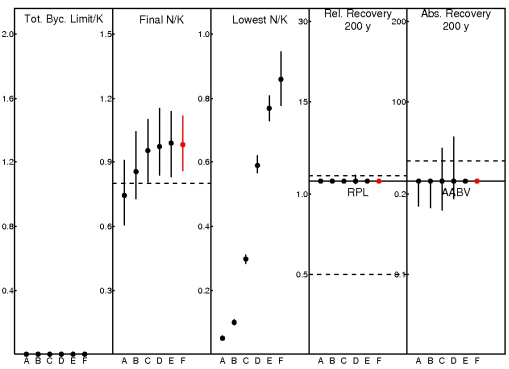
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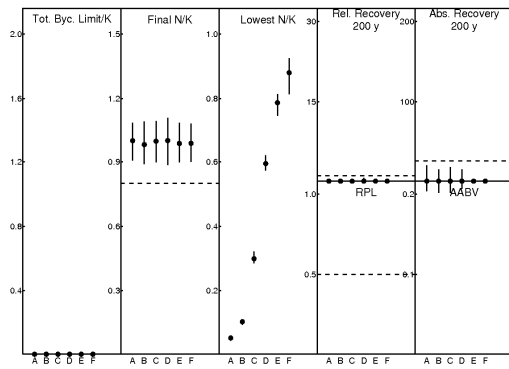
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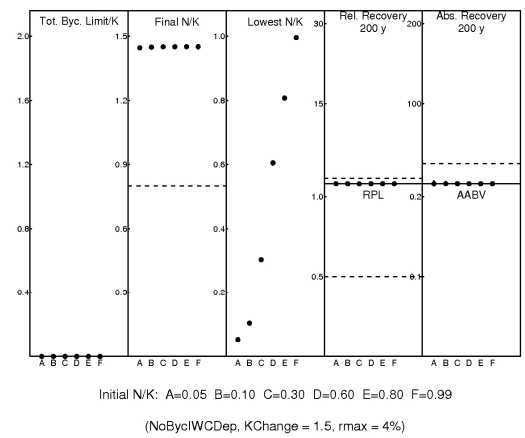
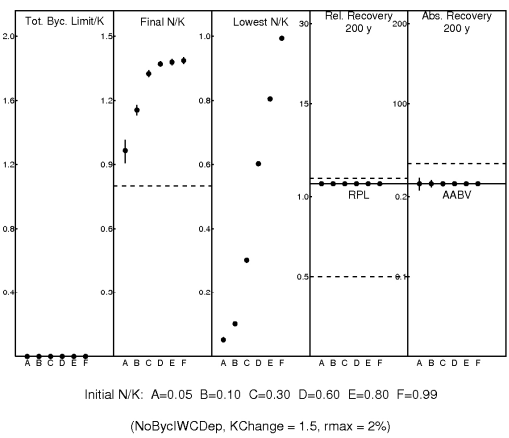
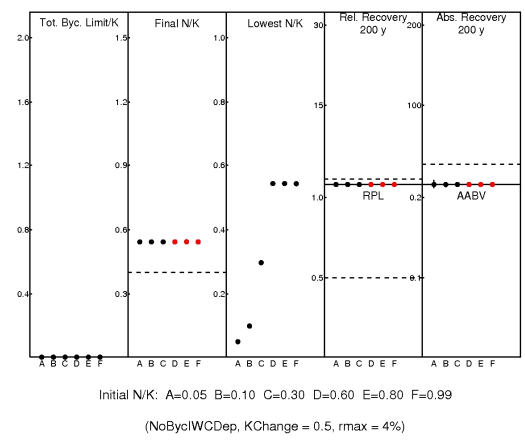
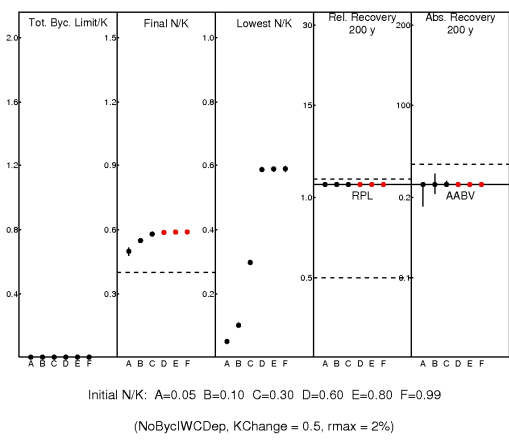
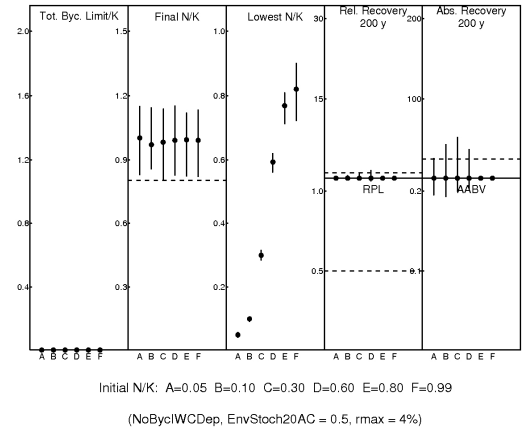
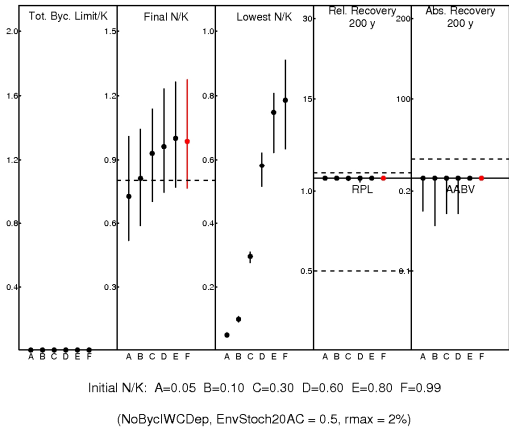
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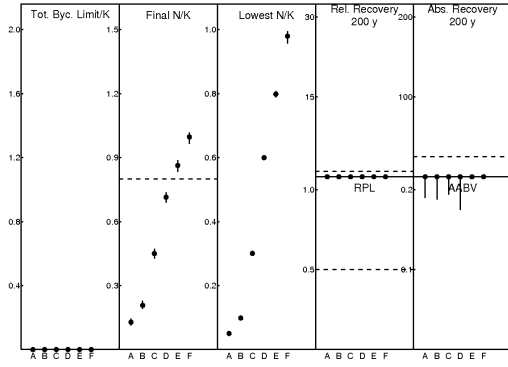


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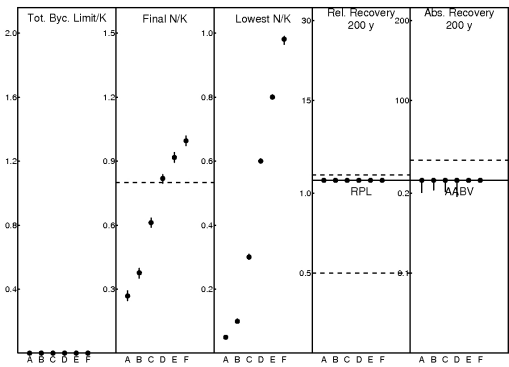


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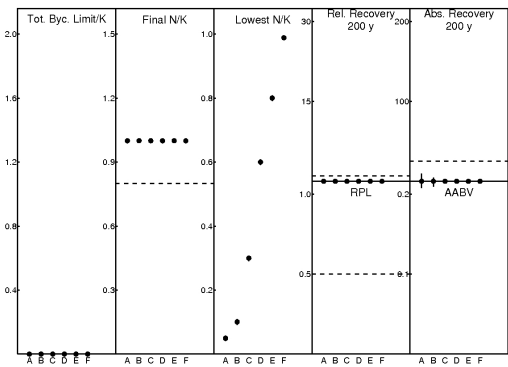




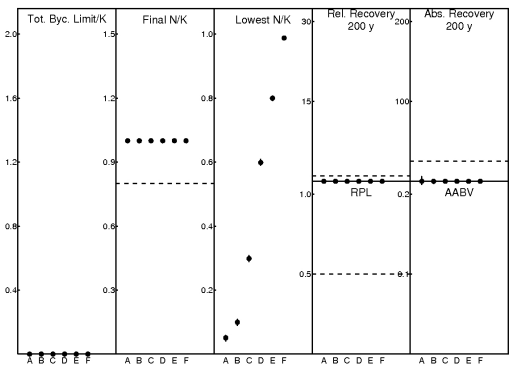
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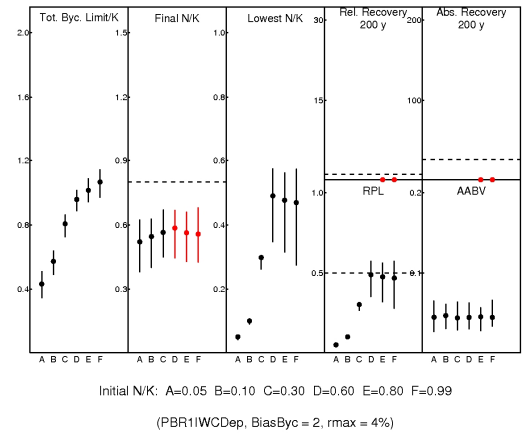
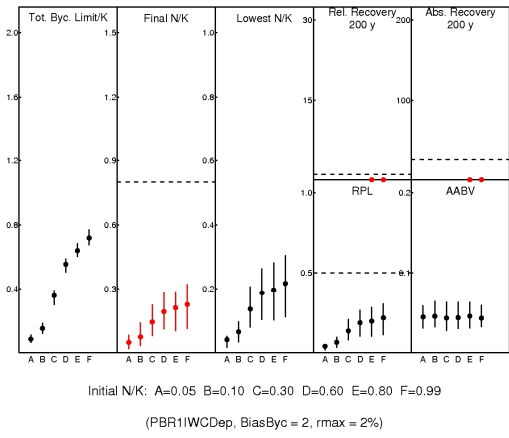
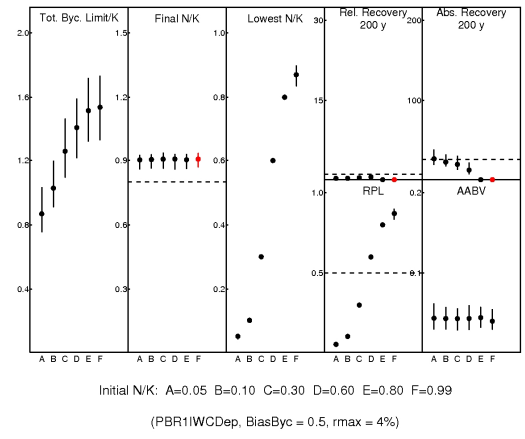
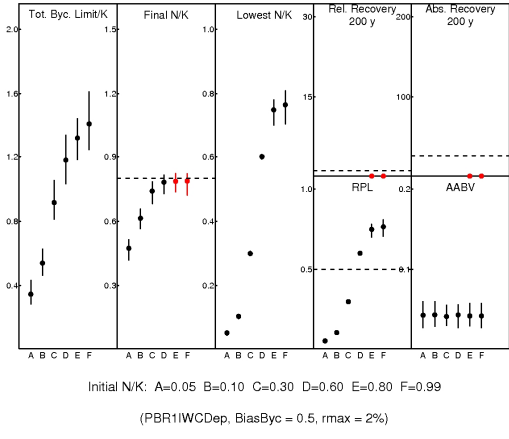
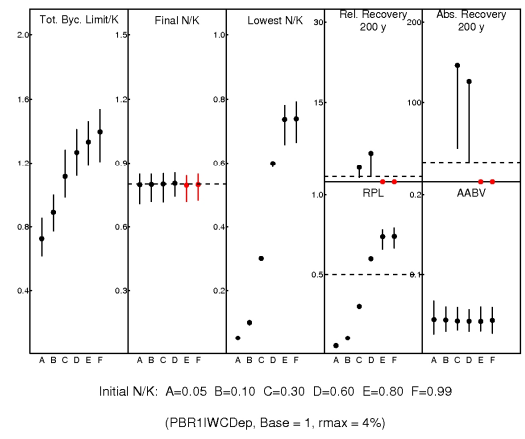
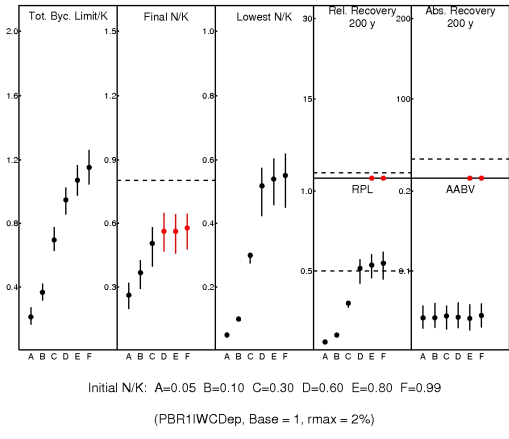
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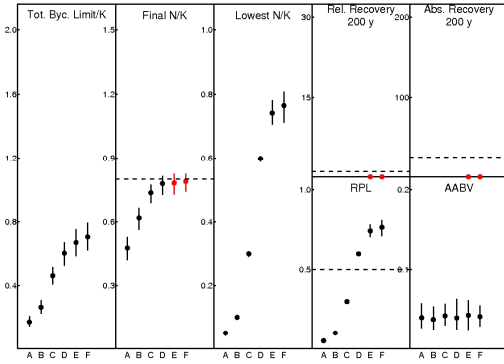


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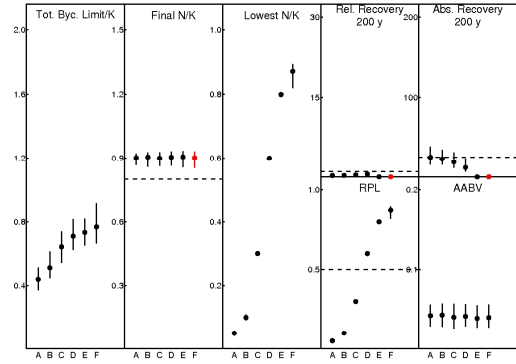


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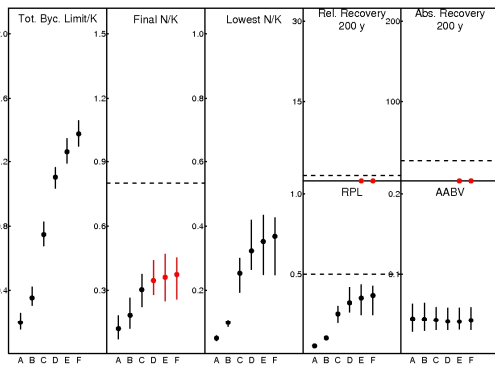




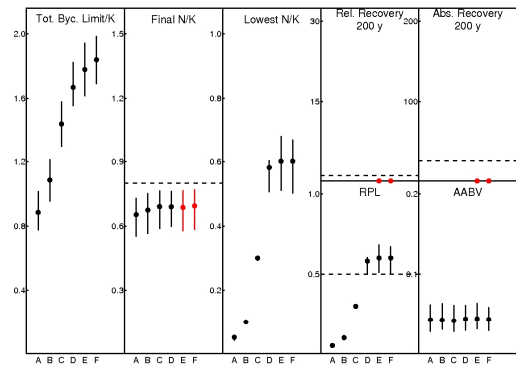
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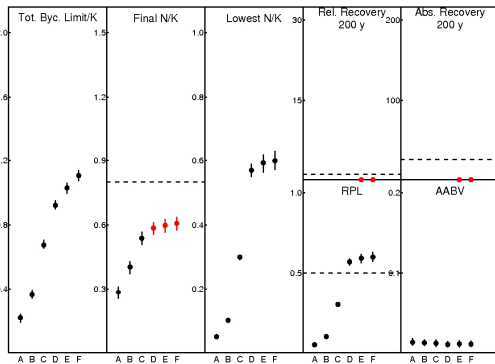
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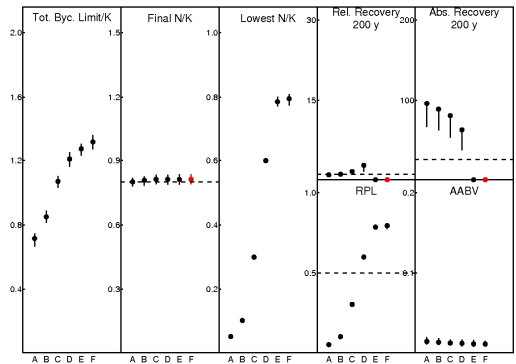
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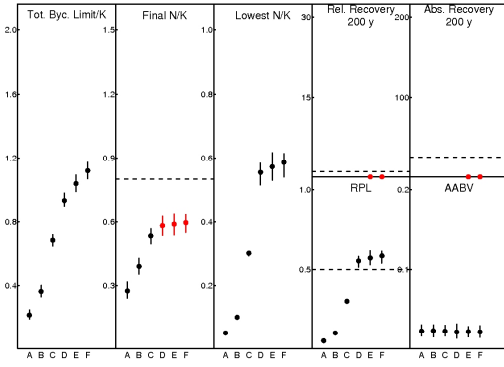
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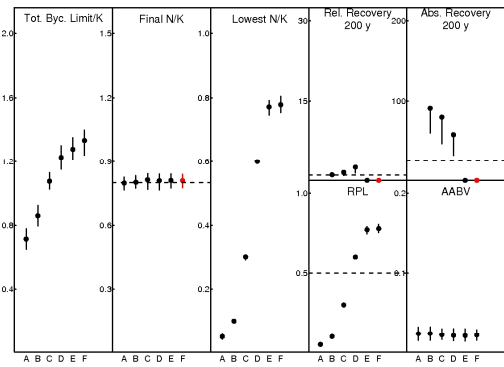
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(PBR1WCDep, BiasSrvyCVAbs = 0.5, rmax = 2%)



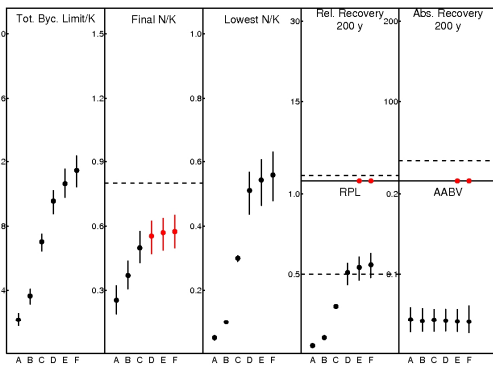
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1WCDep, BiasSrvyCVAbs = 0.5, rmax = 4%)



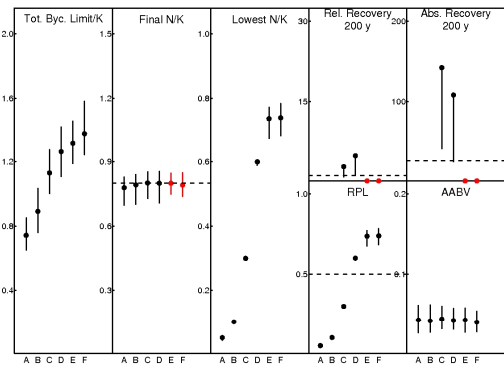
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, BiasSrvyCVAbs = 1, rmax = 2%)



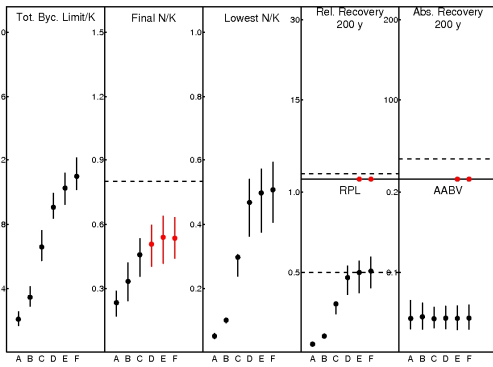
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, BiasSrvyCVAbs = 1, rmax = 4%)



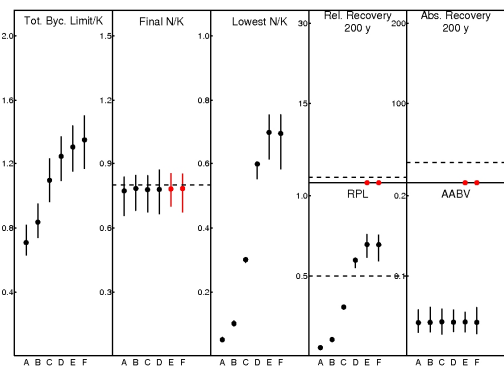
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, BycCV = 0.1, rmax = 2%)



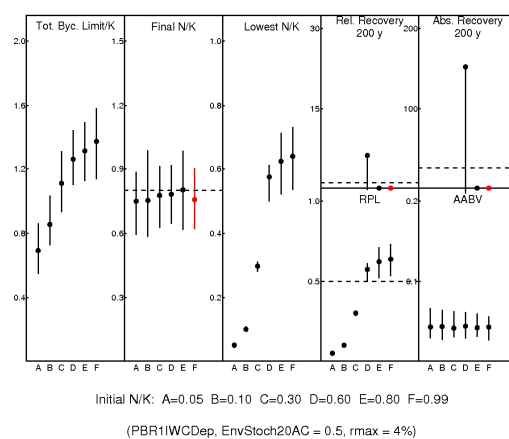
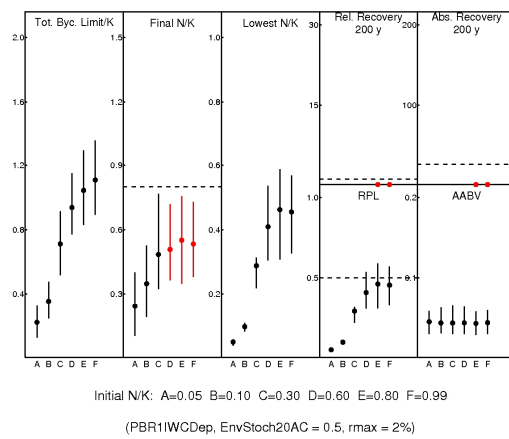
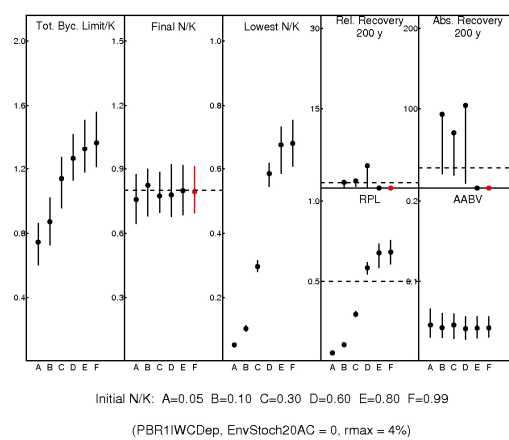
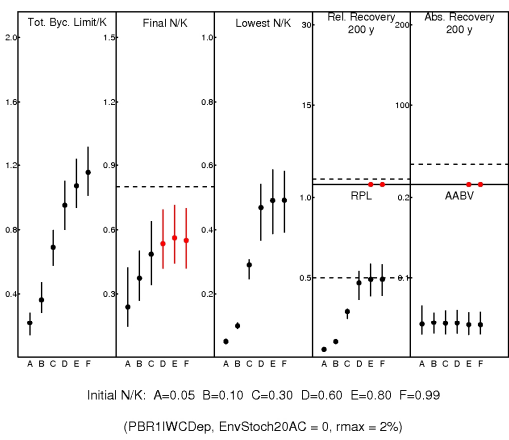
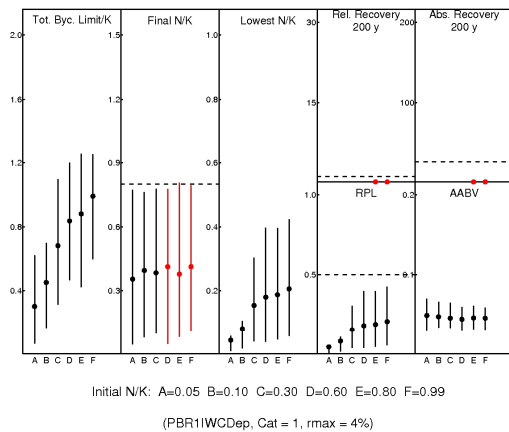
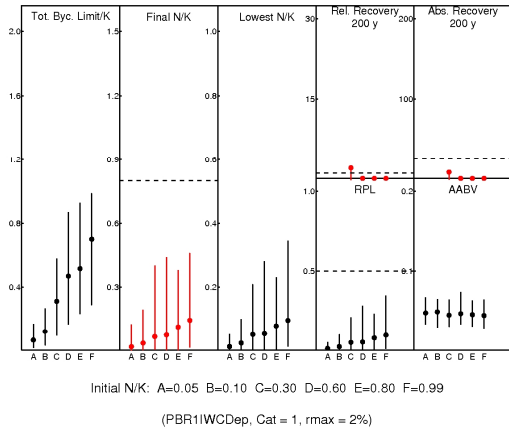
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, BycCV = 0.1, rmax = 4%)

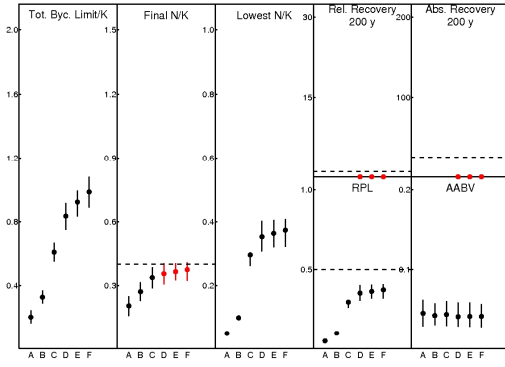


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, BycCV = 1, rmax = 2%)

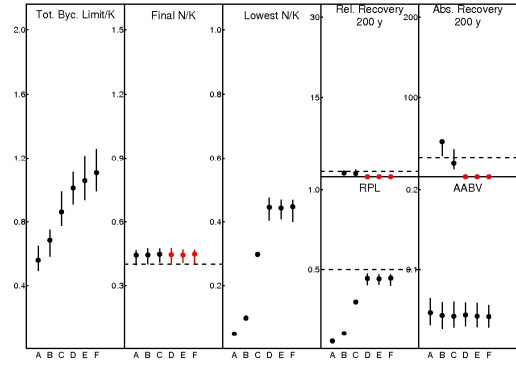


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, BycCV = 1, rmax = 4%)

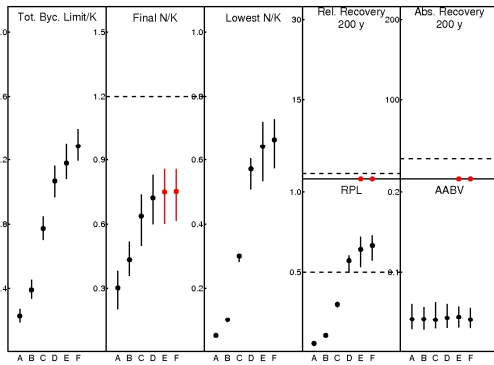




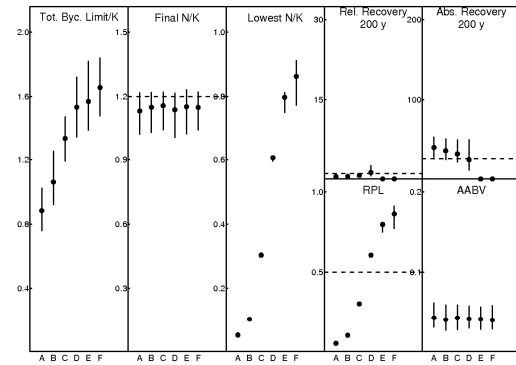
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR11WCDep, KChange = 0.5, rmax = 2%)



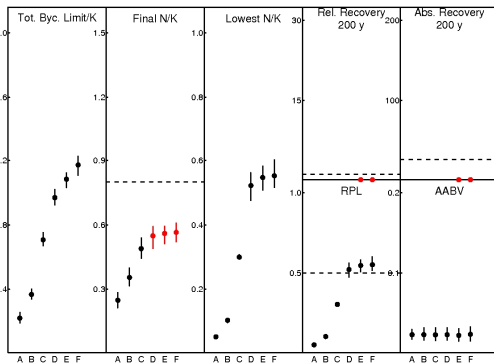
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR11WCDep, KChange = 0.5, rmax = 4%)



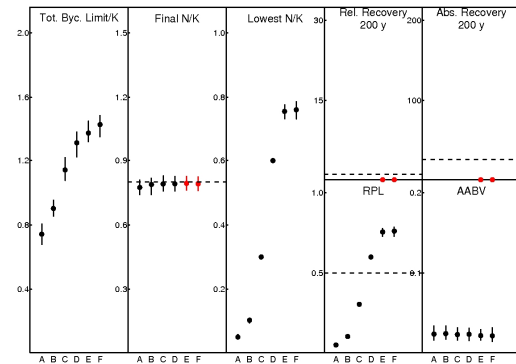
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR11WCDep, KChange = 1.5, rmax = 2%)



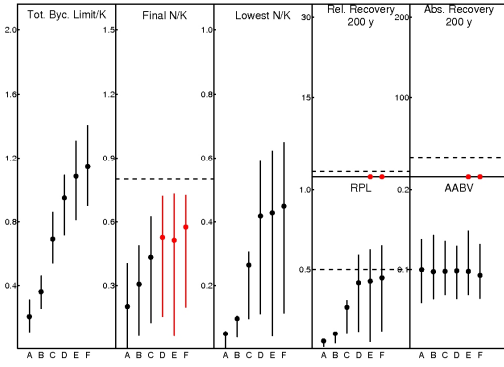
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR11WCDep, KChange = 1.5, rmax = 4%)



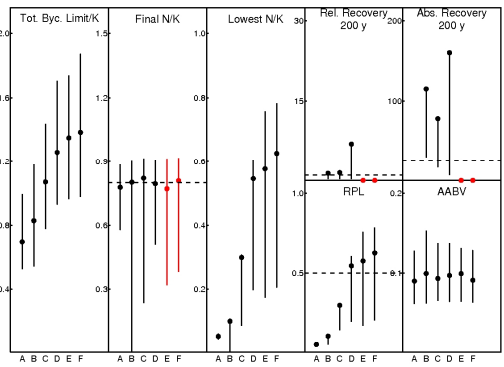
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR11WCDep, SrvyCVAbs = 0.1, rmax = 2%)



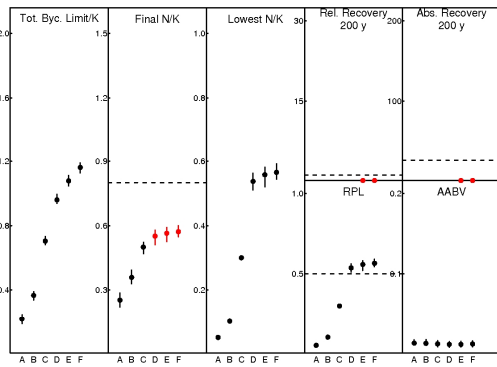
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR11WCDep, SrvyCVAbs = 0.1, rmax = 4%)



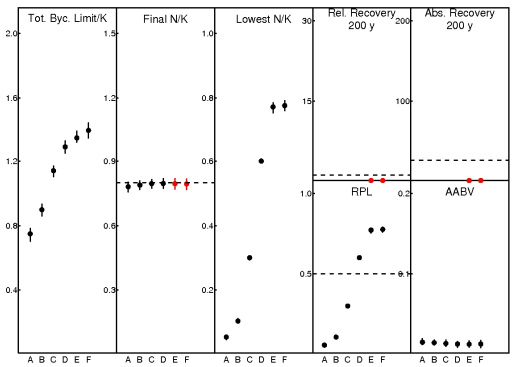
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, SrvyCVAbs = 0.6, rmax = 2%)



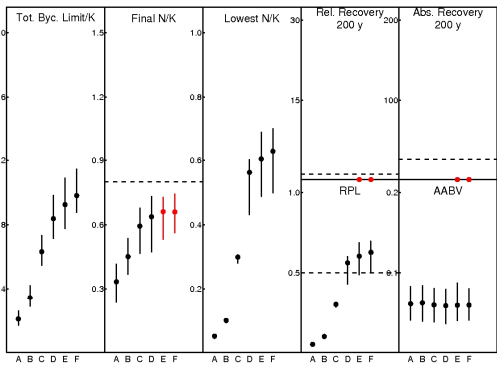
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, SrvyCVAbs = 0.6, rmax = 4%)



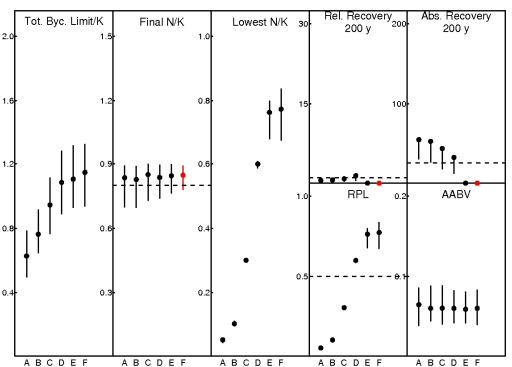
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, SrvyCVAbsUnbias = 0.1, rmax = 2%)



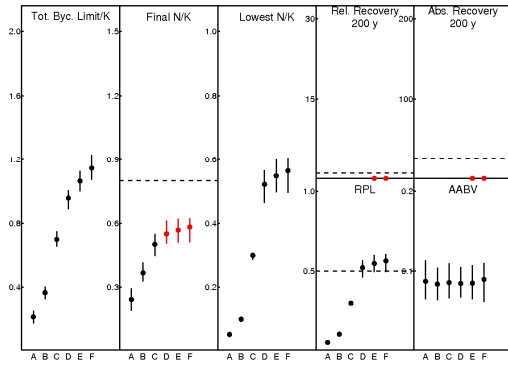
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, SrvyCVAbsUnbias = 0.1, rmax = 4%)



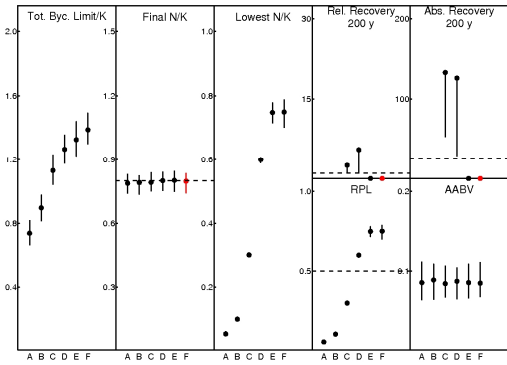
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, SrvyCVAbsUnbias = 0.6, rmax = 2%)



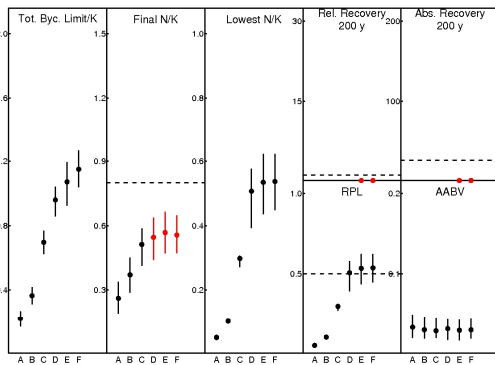
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, SrvyCVAbsUnbias = 0.6, rmax = 4%)



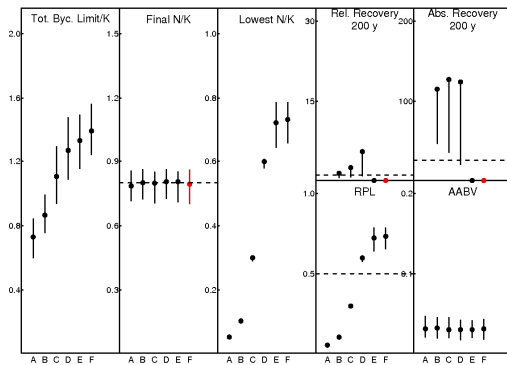
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, SrvyFreq = 5, rmax = 2%)



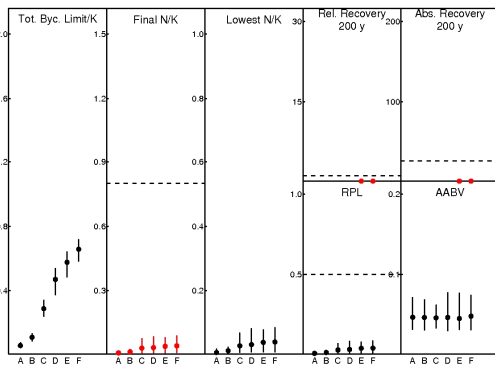
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, SrvyFreq = 5, rmax = 4%)



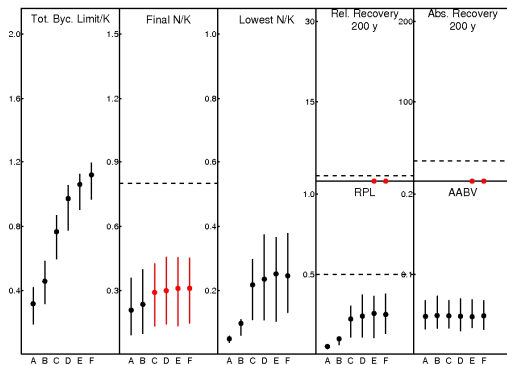
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, SrvyFreq = 15, rmax = 2%)



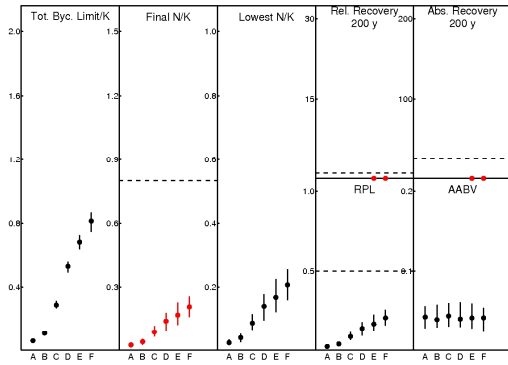
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, SrvyFreq = 15, rmax = 4%)



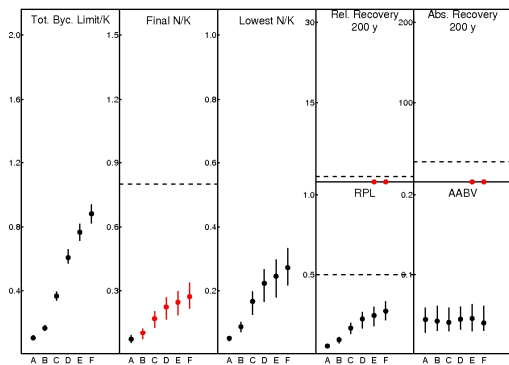
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, WorstCase = 1, rmax = 2%)



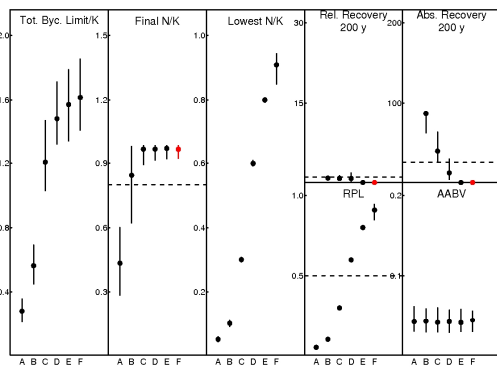
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1IWCDep, WorstCase = 1, rmax = 4%)



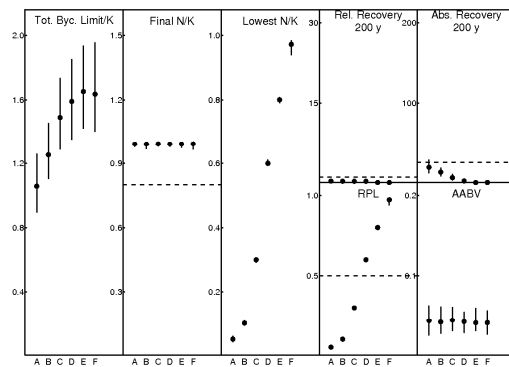
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1WCDep, z = 0.1, rmax = 2%)



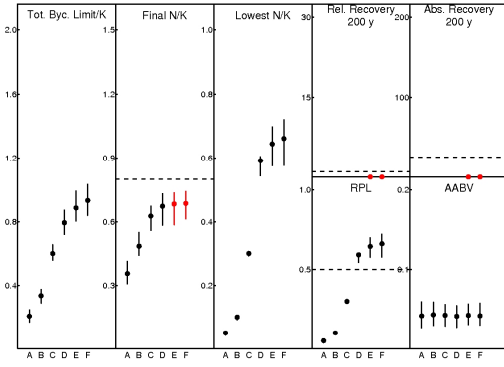
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1WCDep, z = 0.1, rmax = 4%)



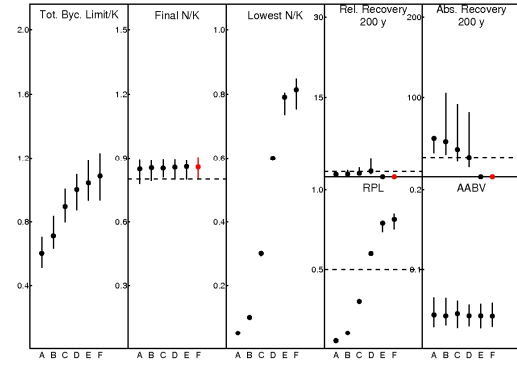
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1WCDep, z = 13.5, rmax = 2%)



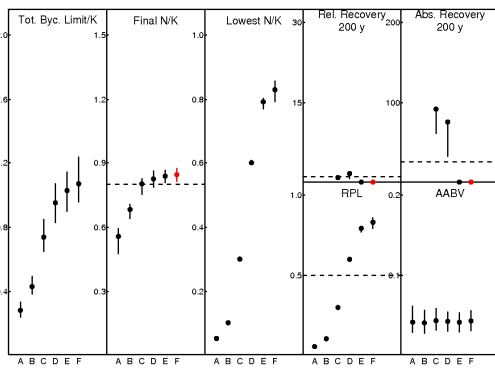
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR1WCDep, z = 13.5, rmax = 4%)



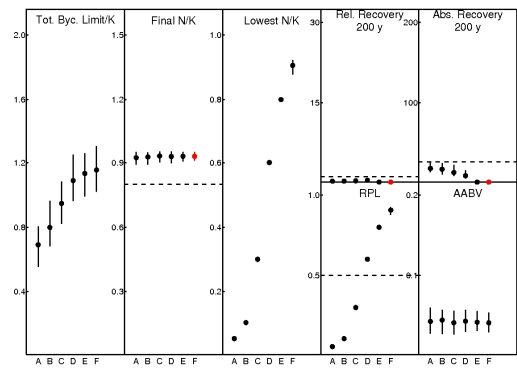
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2WCDep, Base = 1, rmax = 2%)



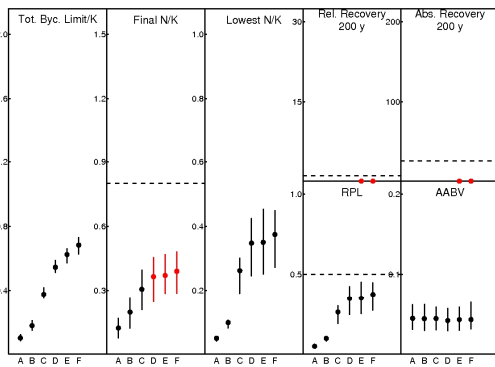
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2WCDep, Base = 1, rmax = 4%)



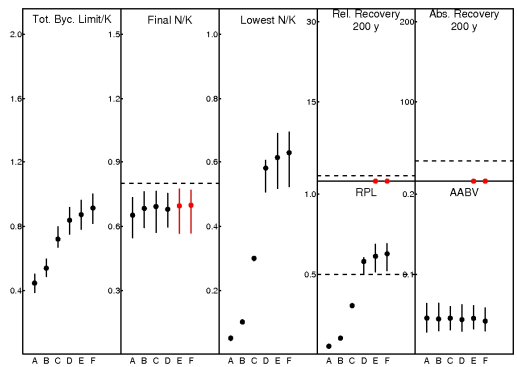
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2WCDep, BiasByc = 0.5, rmax = 2%)



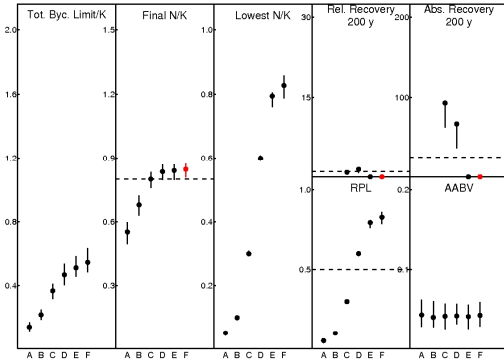
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2WCDep, BiasByc = 0.5, rmax = 4%)



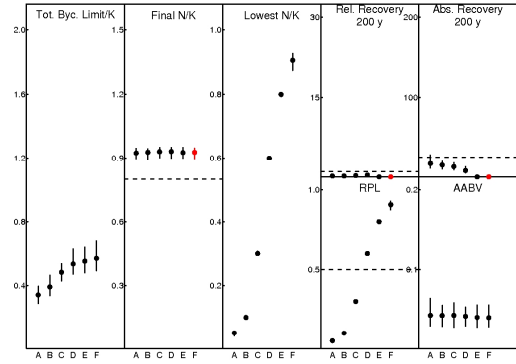
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2WCDep, BiasByc = 2, rmax = 2%)



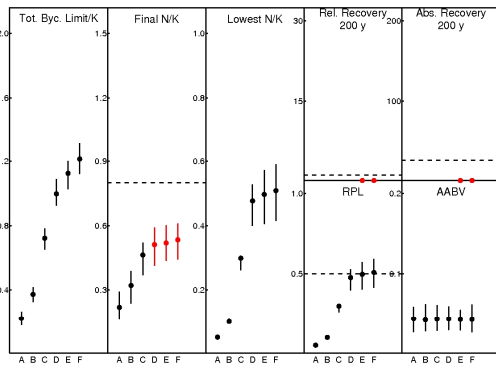
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2WCDep, BiasByc = 2, rmax = 4%)



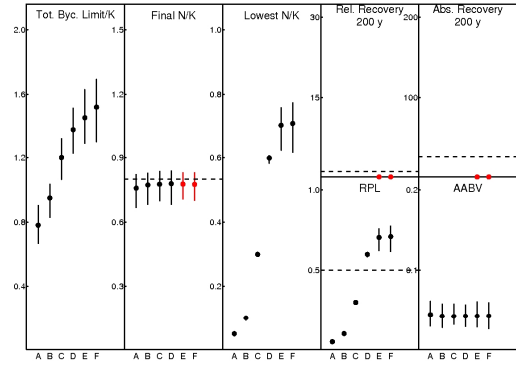
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, BiasSrvyAbs = 0.5, rmax = 2%)



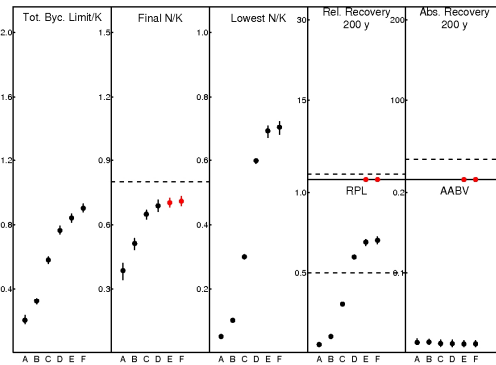
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, BiasSrvyAbs = 0.5, rmax = 4%)



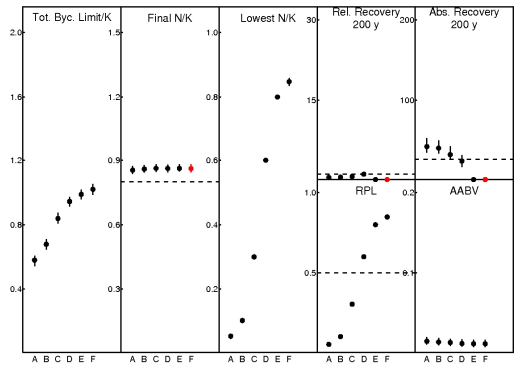
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, BiasSrvyAbs = 1.5, rmax = 2%)



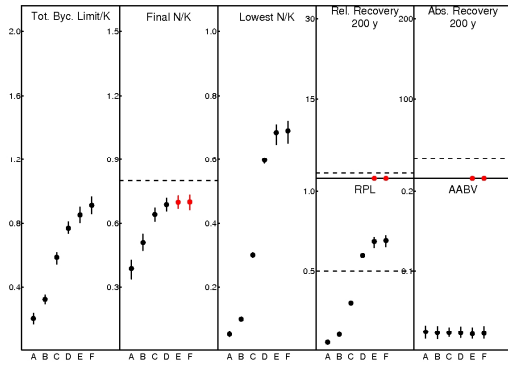
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, BiasSrvyAbs = 1.5, rmax = 4%)



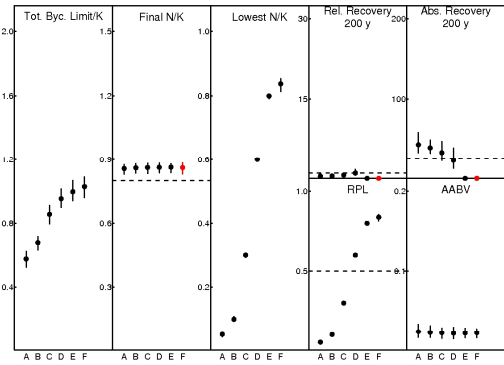
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, BiasSrvyCVAbs = 0.5, rmax = 2%)



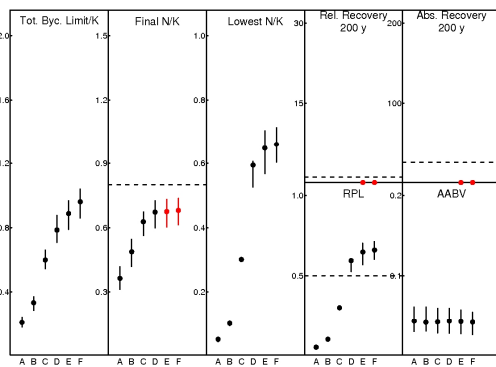
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, BiasSrvyCVAbs = 0.5, rmax = 4%)



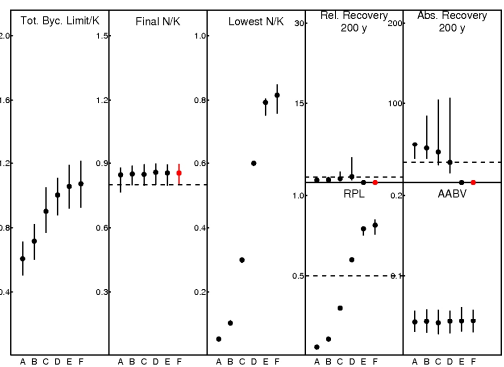
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, BiasSrvyCVAbs = 1, rmax = 2%)



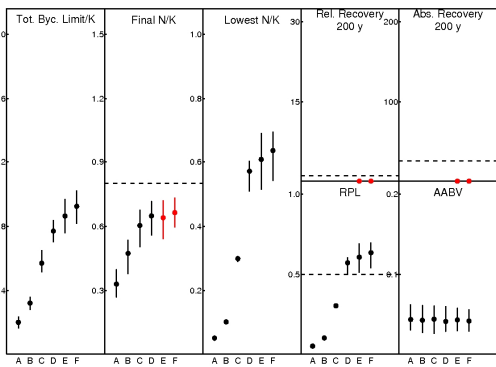
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, BiasSrvyCVAbs = 1, rmax = 4%)



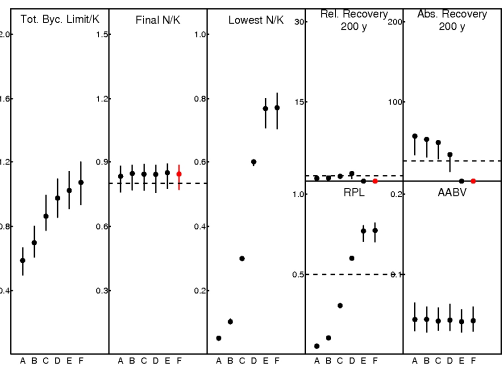
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, BycCV = 0.1, rmax = 2%)



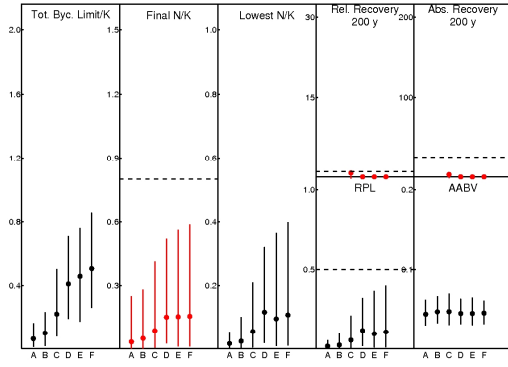
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, BycCV = 0.1, rmax = 4%)



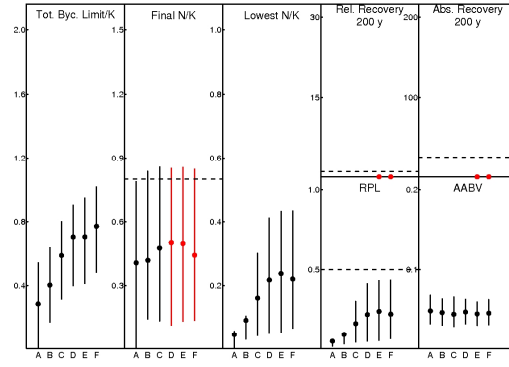
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, BycCV = 1, rmax = 2%)



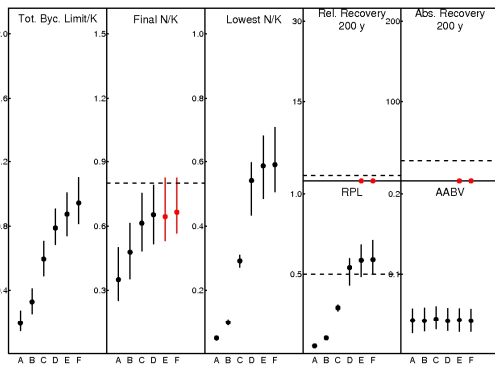
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, BycCV = 1, rmax = 4%)



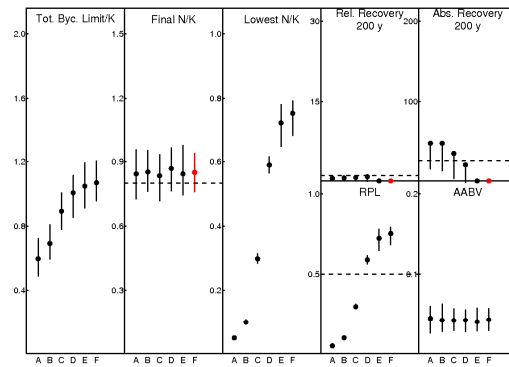
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, Cat = 1, rmax = 2%)



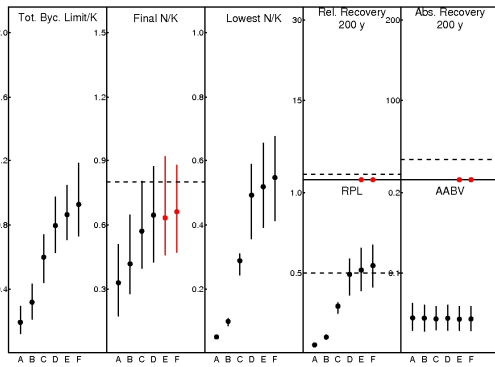
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, Cat = 1, rmax = 4%)



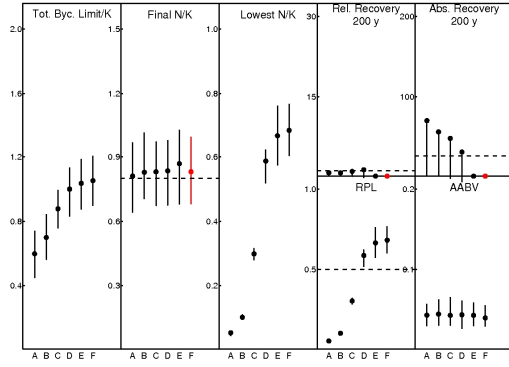
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, EnvStoch20AC = 0, rmax = 2%)



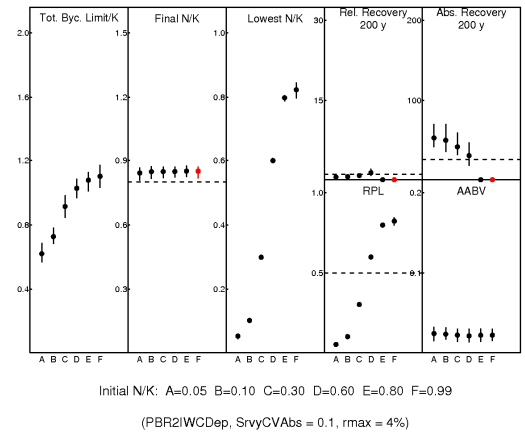
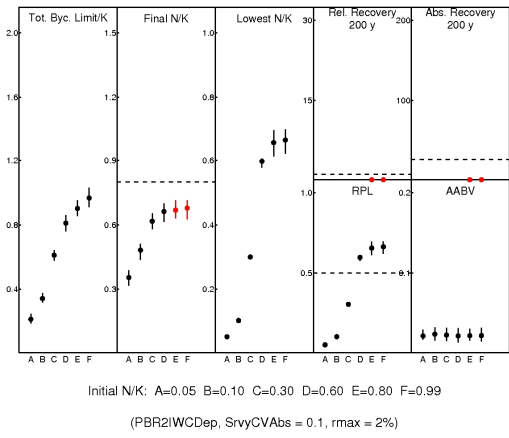
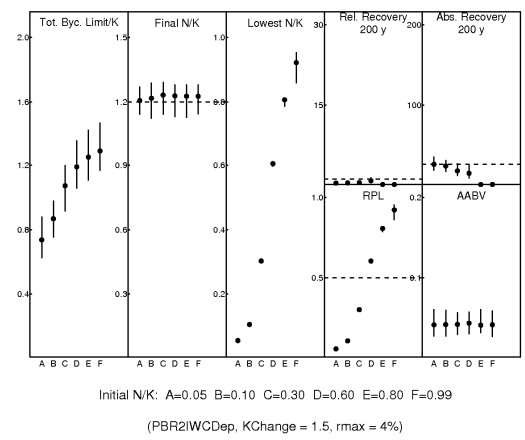
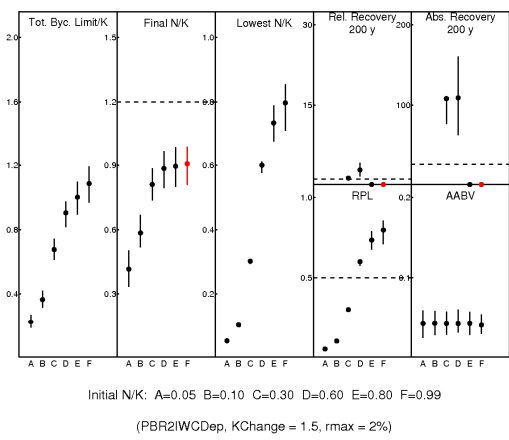
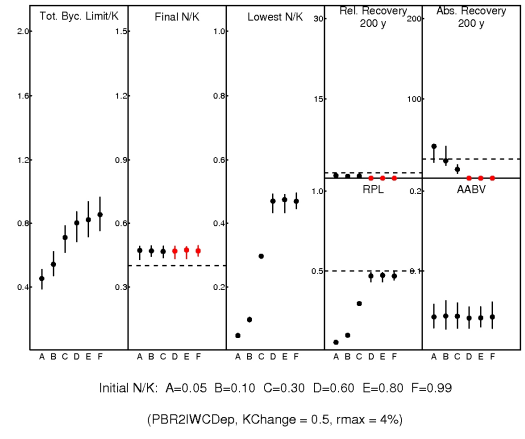
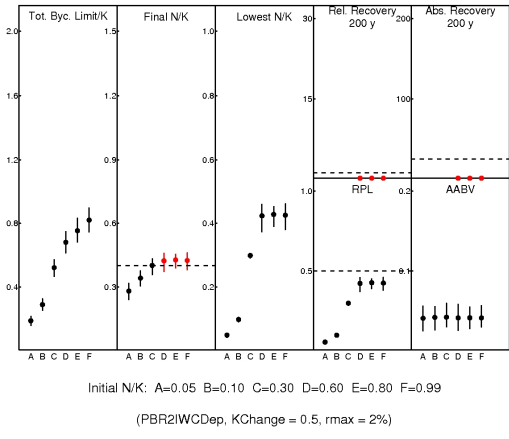
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, EnvStoch20AC = 0, rmax = 4%)

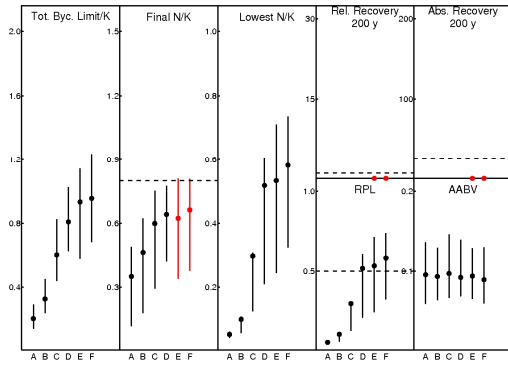


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, EnvStoch20AC = 0.5, rmax = 2%)

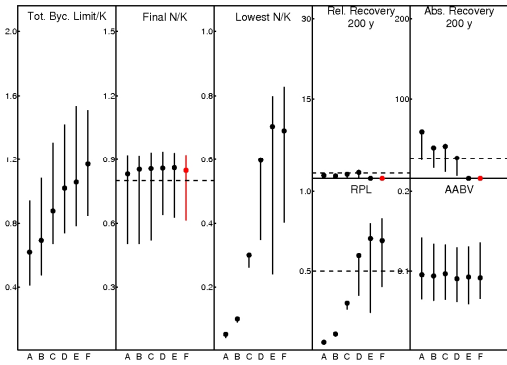


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, EnvStoch20AC = 0.5, rmax = 4%)

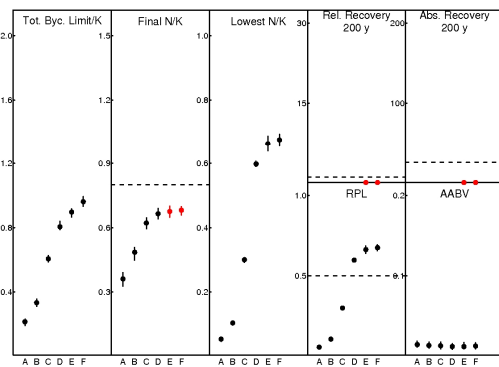




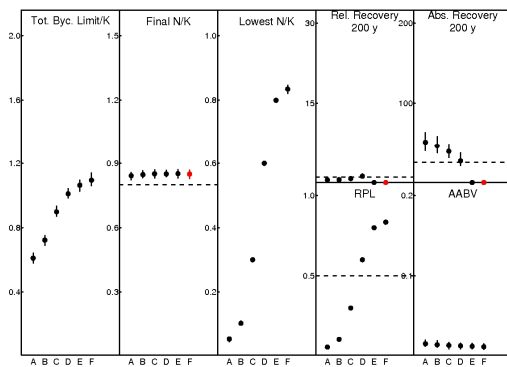
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, SrvyCVAbs = 0.6, rmax = 2%)



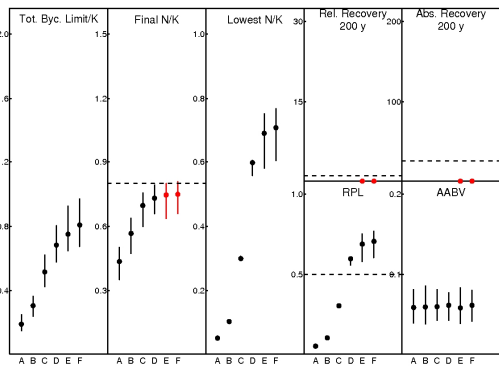
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, SrvyCVAbs = 0.6, rmax = 4%)



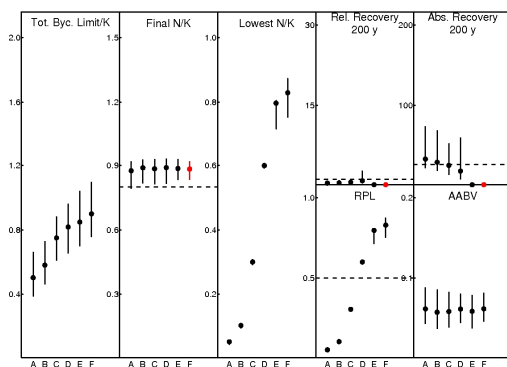
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, SrvyCVAbsUnbias = 0.1, rmax = 2%)



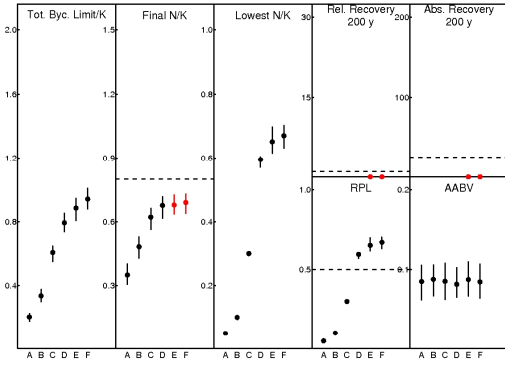
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, SrvyCVAbsUnbias = 0.1, rmax = 4%)



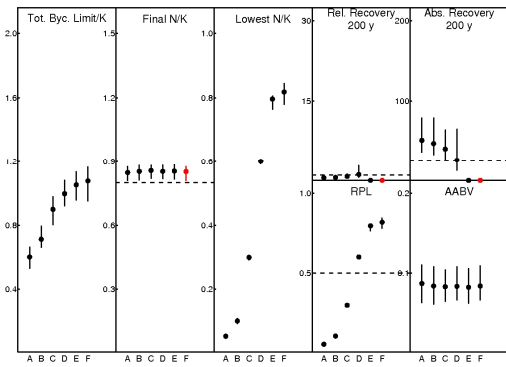
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, SrvyCVAbsUnbias = 0.6, rmax = 2%)



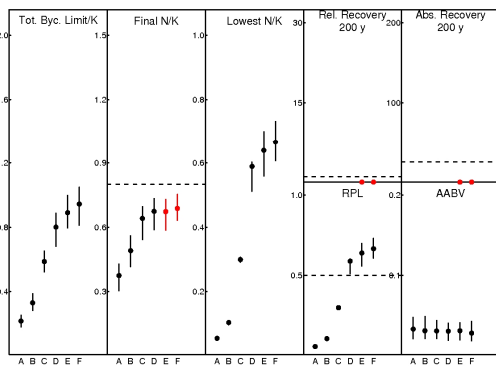
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, SrvyCVAbsUnbias = 0.6, rmax = 4%)



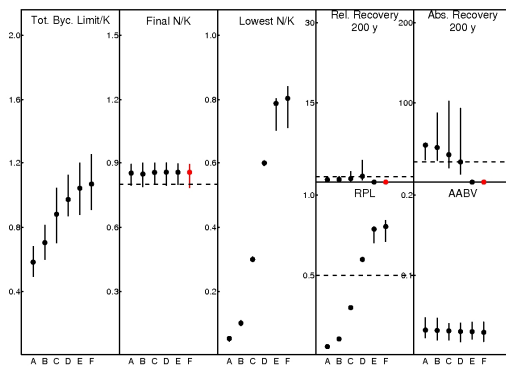
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, SrvyFreq = 5, rmax = 2%)



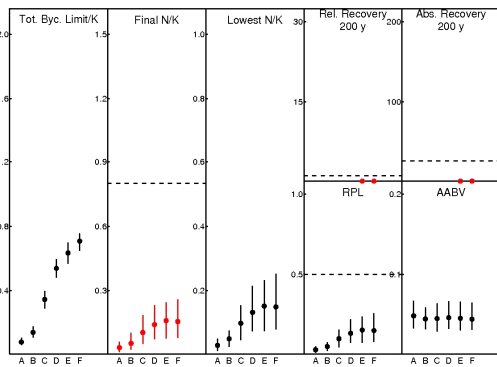
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, SrvyFreq = 5, rmax = 4%)



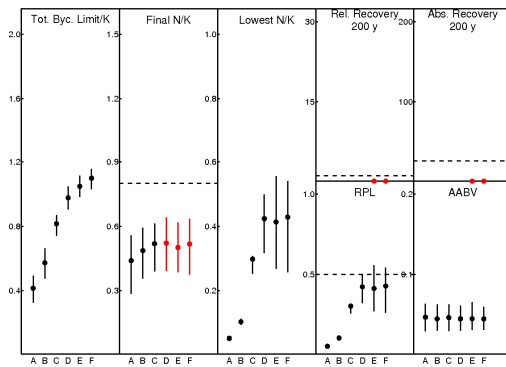
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, SrvyFreq = 15, rmax = 2%)



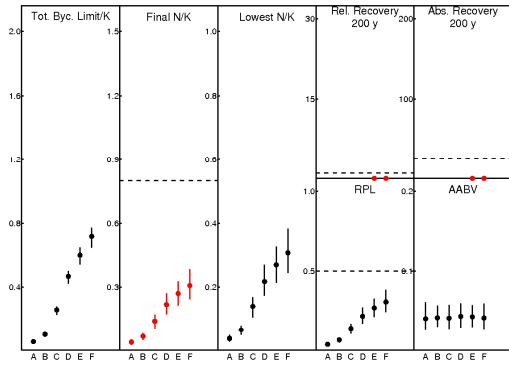
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, SrvyFreq = 15, rmax = 4%)



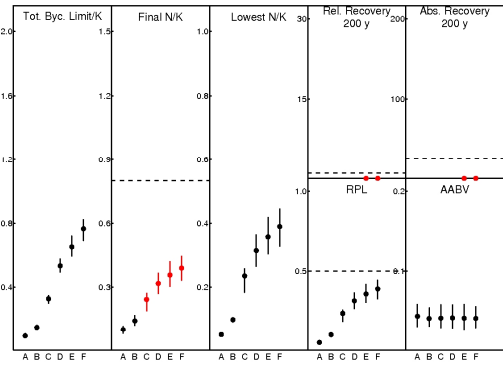
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, WorstCase = 1, rmax = 2%)



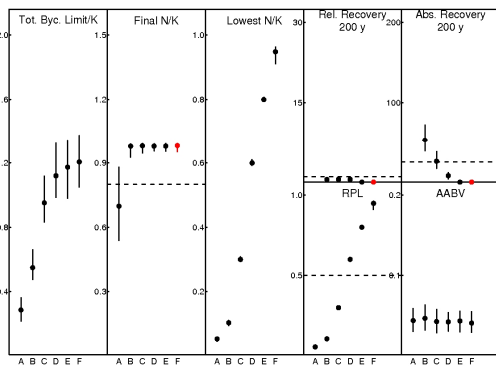
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, WorstCase = 1, rmax = 4%)



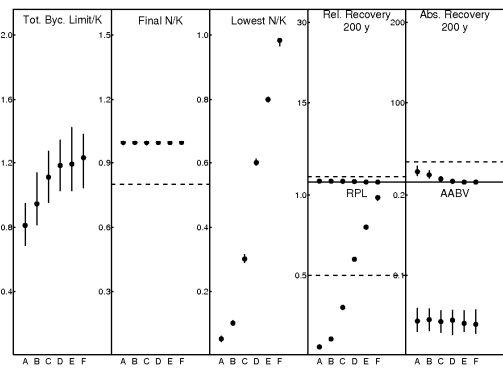
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, z = 0.1, rmax = 2%)



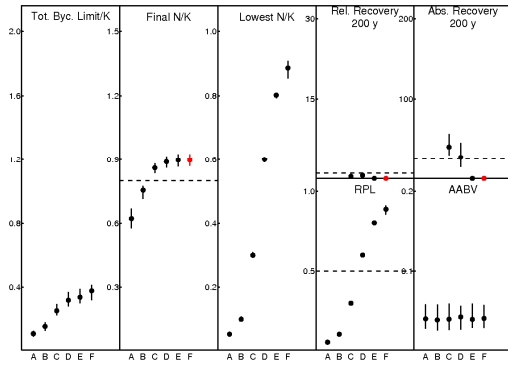
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, z = 0.1, rmax = 4%)



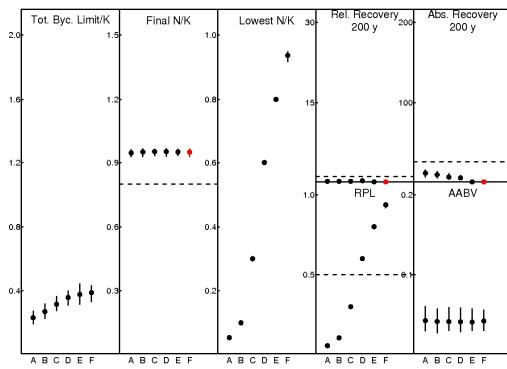
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, z = 13.5, rmax = 2%)



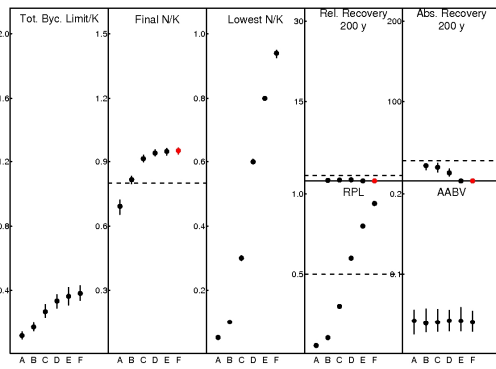
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR2IWCDep, z = 13.5, rmax = 4%)



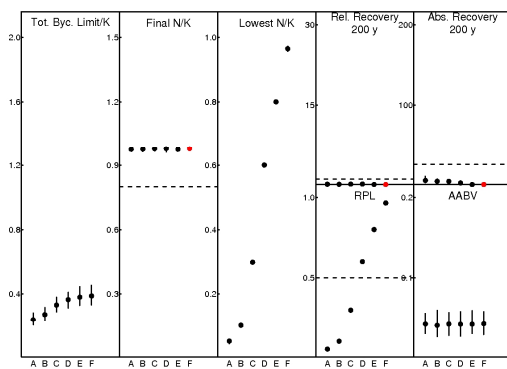
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, Base = 1, rmax = 2%)



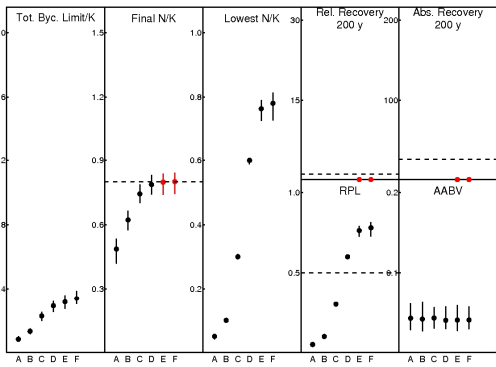
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, Base = 1, rmax = 4%)



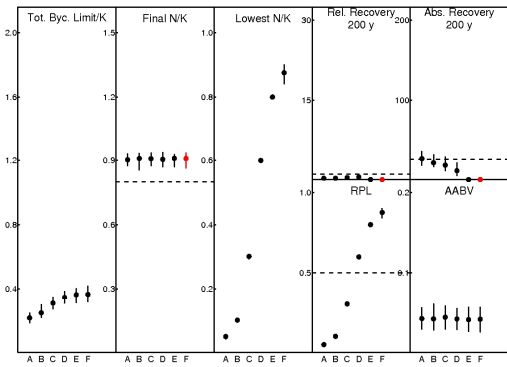
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, BiasByc = 0.5, rmax = 2%)



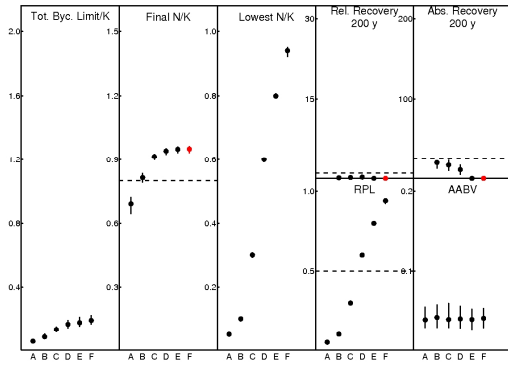
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, BiasByc = 0.5, rmax = 4%)



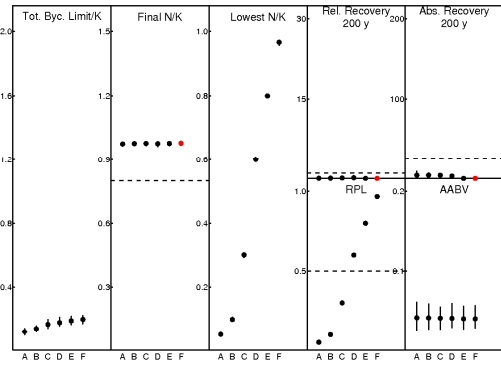
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, BiasByc = 2, rmax = 2%)



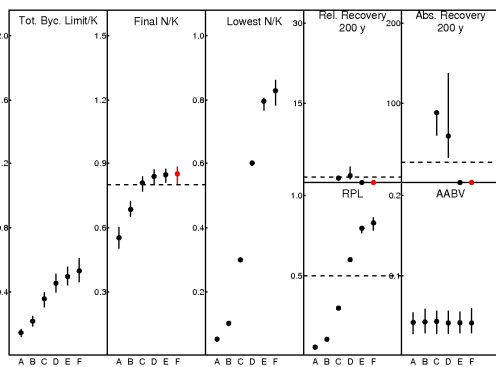
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, BiasByc = 2, rmax = 4%)



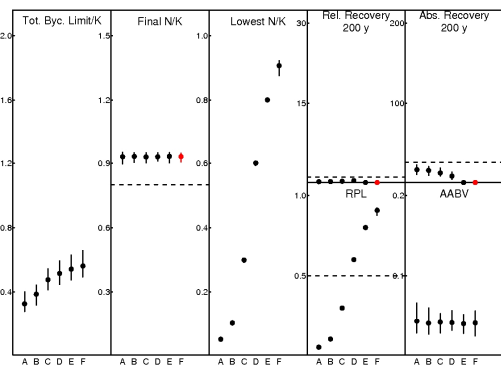
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, BiasSrvyAbs = 0.5, rmax = 2%)



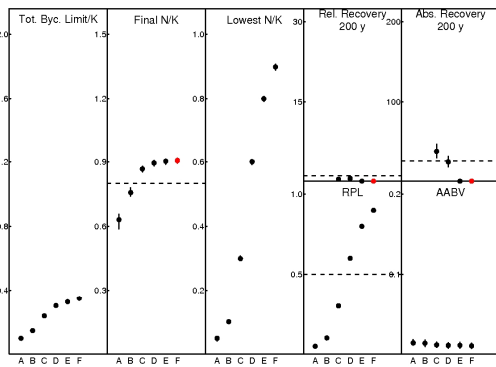
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, BiasSrvyAbs = 0.5, rmax = 4%)



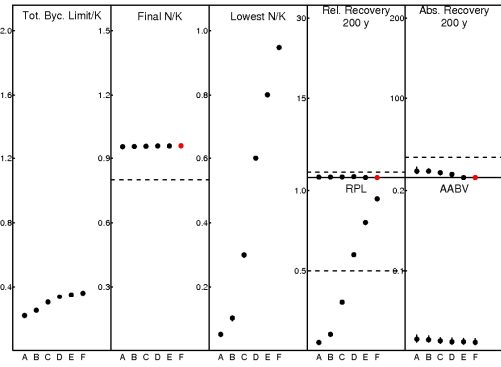
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, BiasSrvyAbs = 1.5, rmax = 2%)



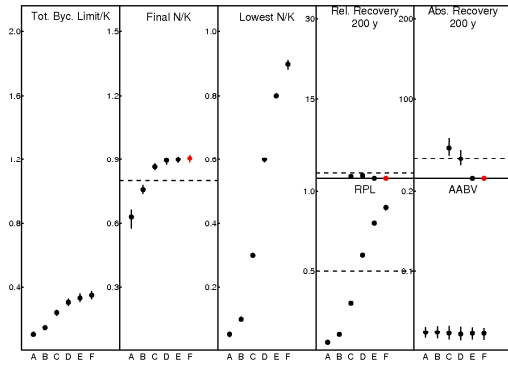
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, BiasSrvyAbs = 1.5, rmax = 4%)



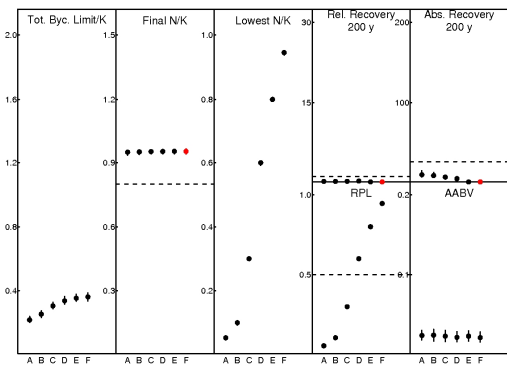
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, BiasSrvyCVAbs = 0.5, rmax = 2%)



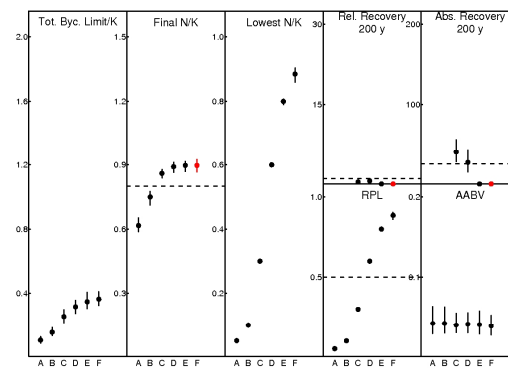
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, BiasSrvyCVAbs = 0.5, rmax = 4%)



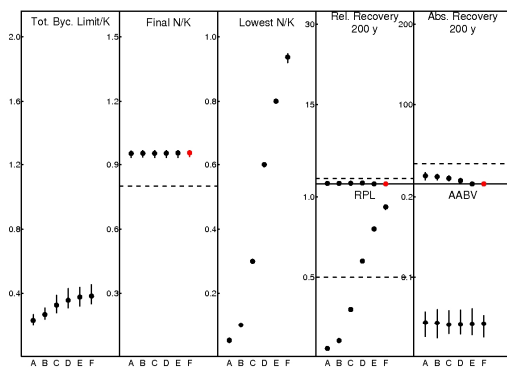
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, BiasSrvyCVAbs = 1, rmax = 2%)



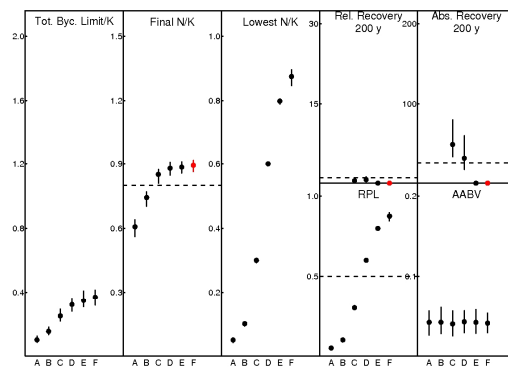
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, BiasSrvyCVAbs = 1, rmax = 4%)



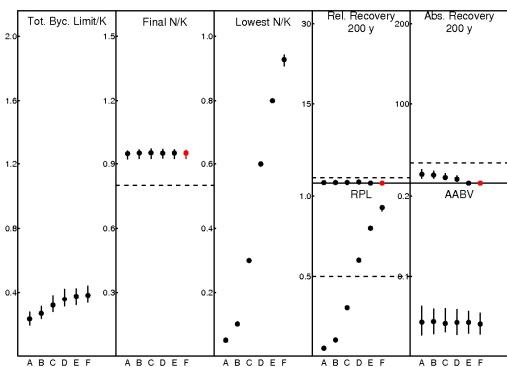
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, BycCV = 0.1, rmax = 2%)



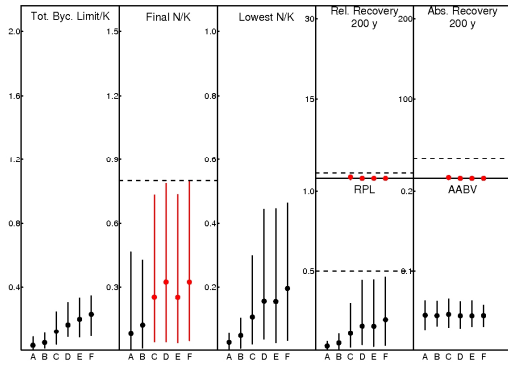
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, BycCV = 0.1, rmax = 4%)



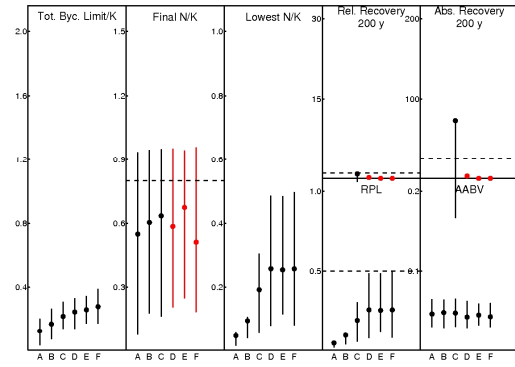
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, BycCV = 1, rmax = 2%)



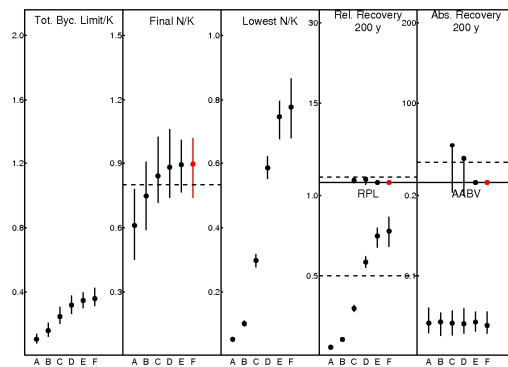
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, BycCV = 1, rmax = 4%)



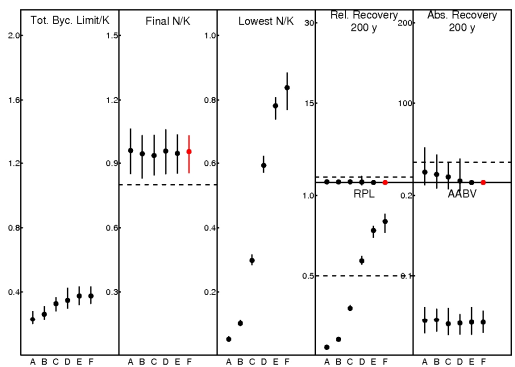
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, Cat = 1, rmax = 2%)



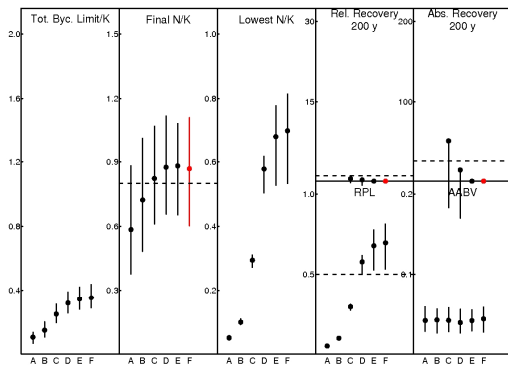
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, Cat = 1, rmax = 4%)



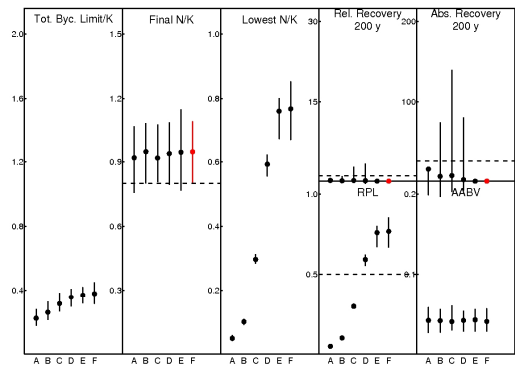
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, EnvStoch20AC = 0, rmax = 2%)



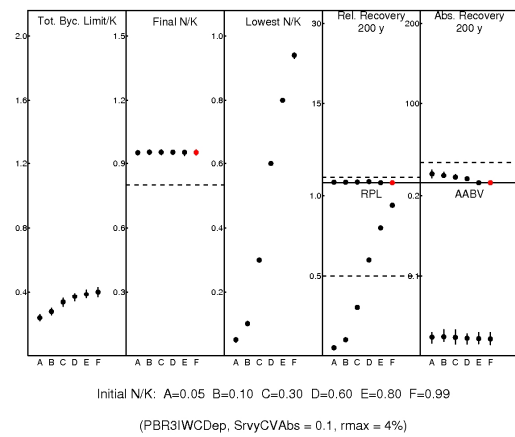
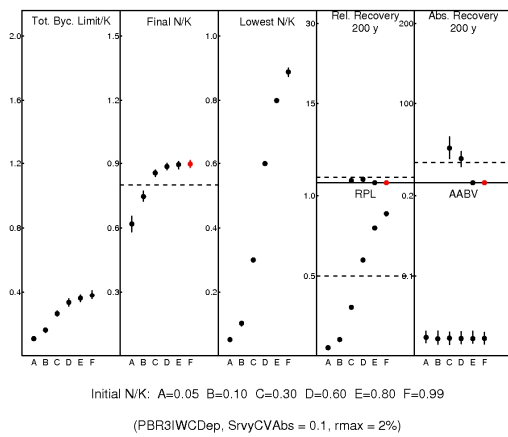
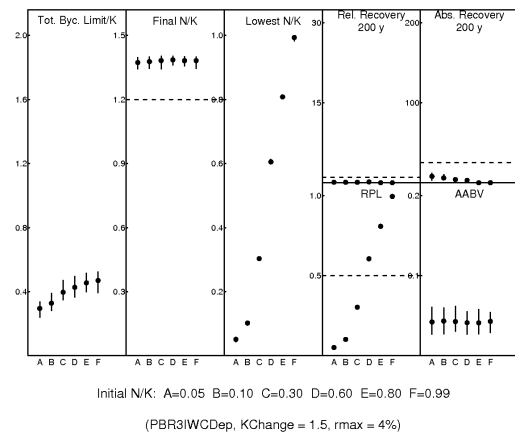
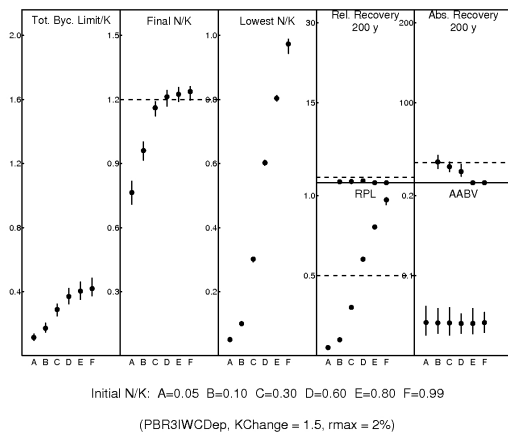
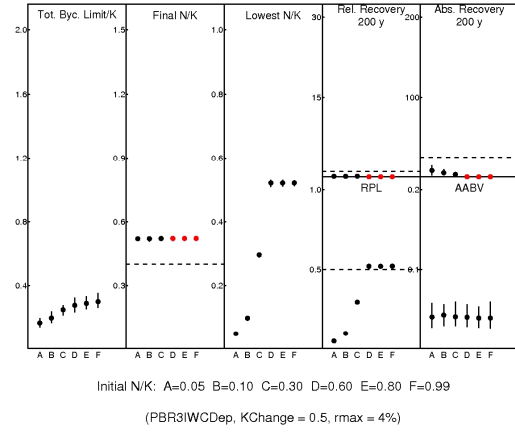
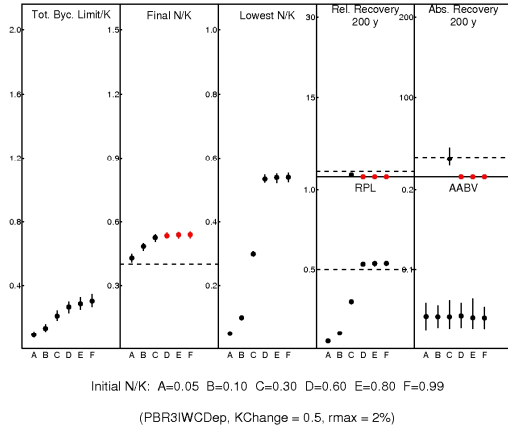
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, EnvStoch20AC = 0, rmax = 4%)

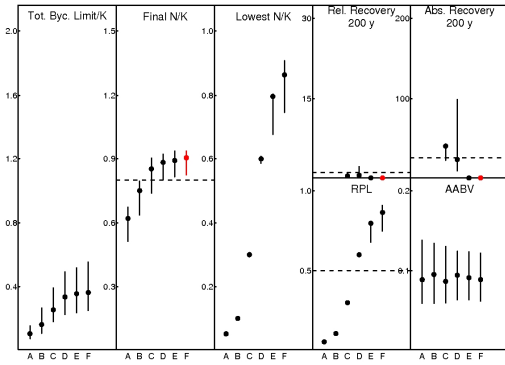


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, EnvStoch20AC = 0.5, rmax = 2%)

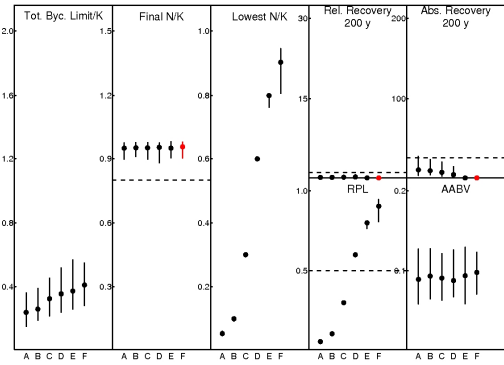


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, EnvStoch20AC = 0.5, rmax = 4%)

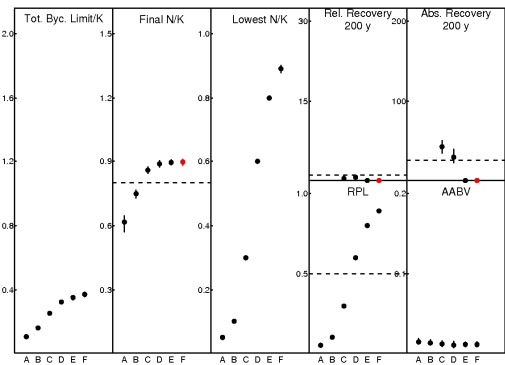




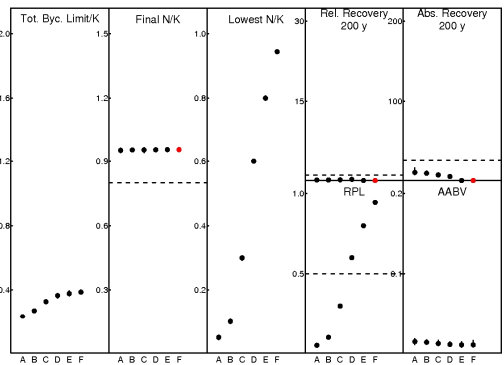
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, SrvyCVAbs = 0.6, rmax = 2%)



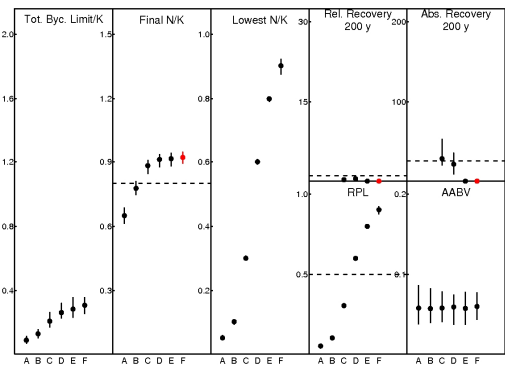
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, SrvyCVAbs = 0.6, rmax = 4%)



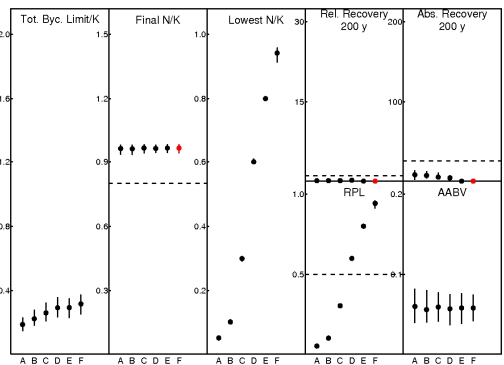
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, SrvyCVAbsUnbias = 0.1, rmax = 2%)



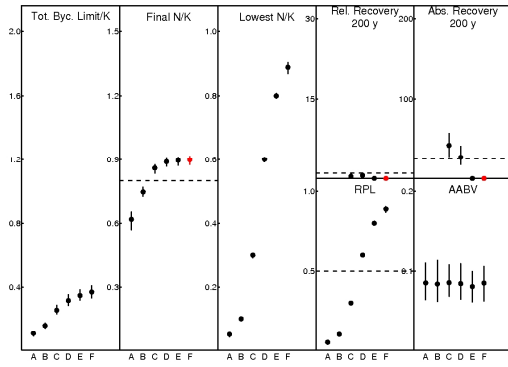
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, SrvyCVAbsUnbias = 0.1, rmax = 4%)



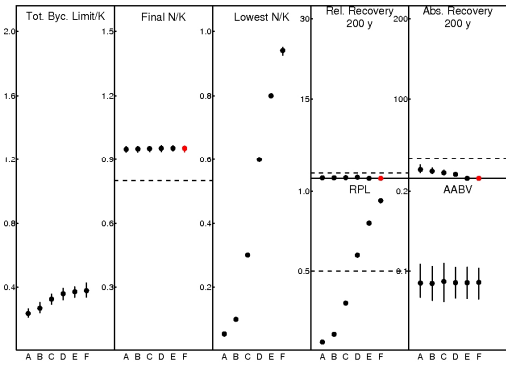
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, SrvyCVAbsUnbias = 0.6, rmax = 2%)



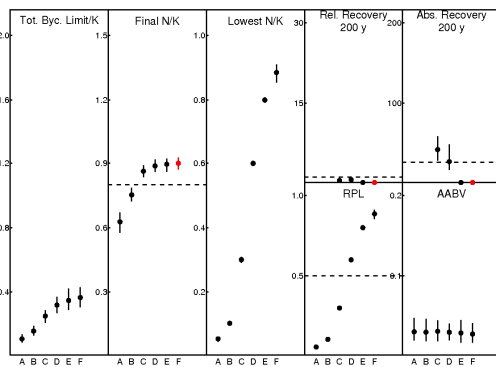
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, SrvyCVAbsUnbias = 0.6, rmax = 4%)



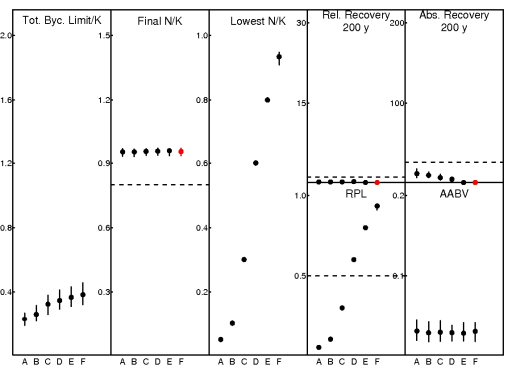
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, SrvyFreq = 5, rmax = 2%)



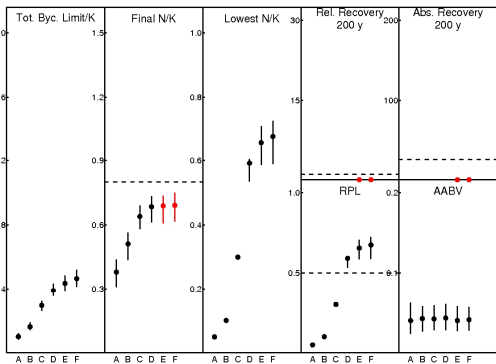
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, SrvyFreq = 5, rmax = 4%)



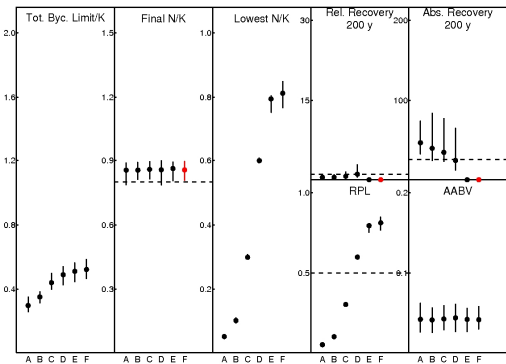
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, SrvyFreq = 15, rmax = 2%)



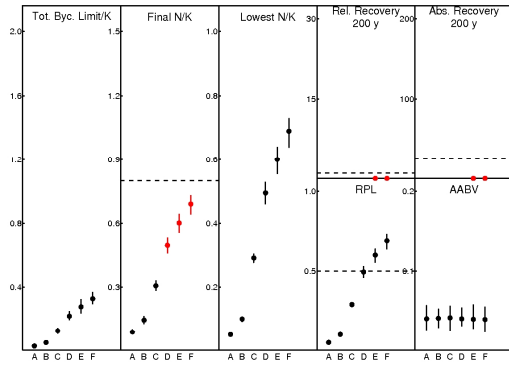
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, SrvyFreq = 15, rmax = 4%)



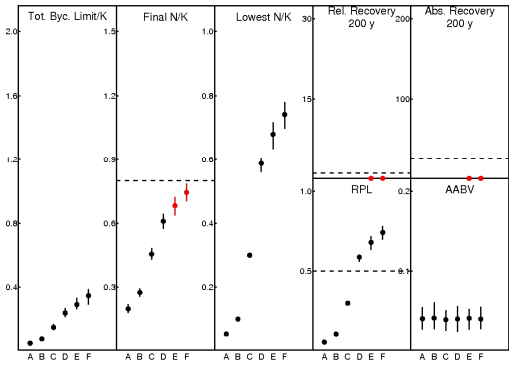
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, WorstCase = 1, rmax = 2%)



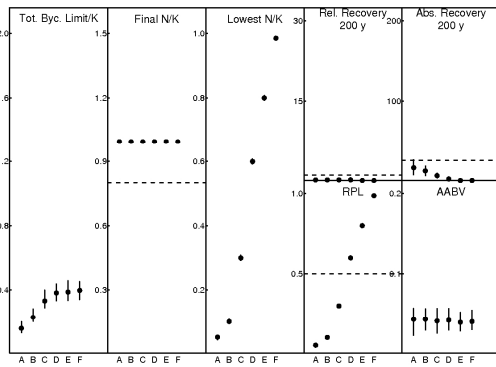
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, WorstCase = 1, rmax = 4%)



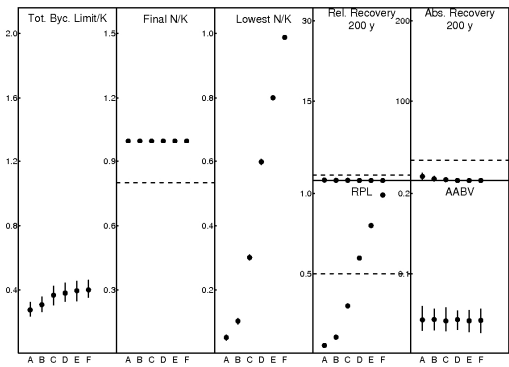
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, z = 0.1, rmax = 2%)



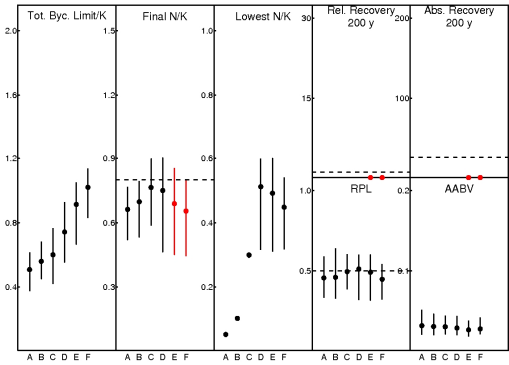
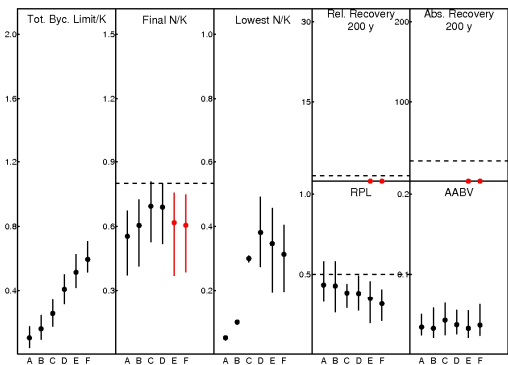
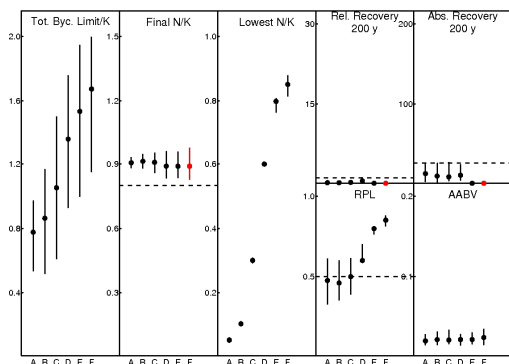
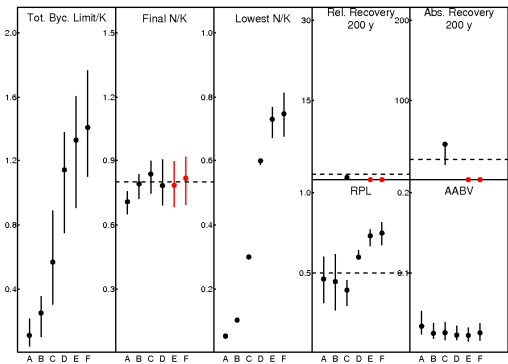
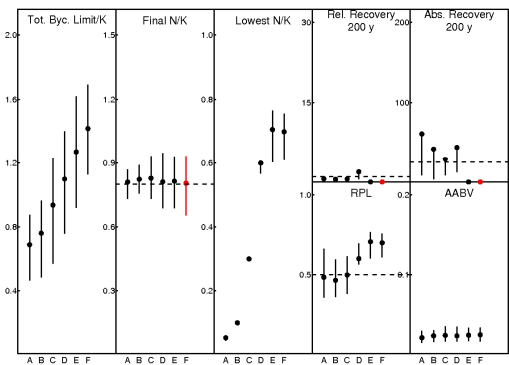
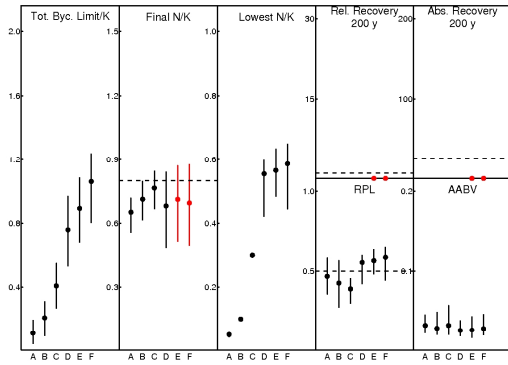
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, z = 0.1, rmax = 4%)

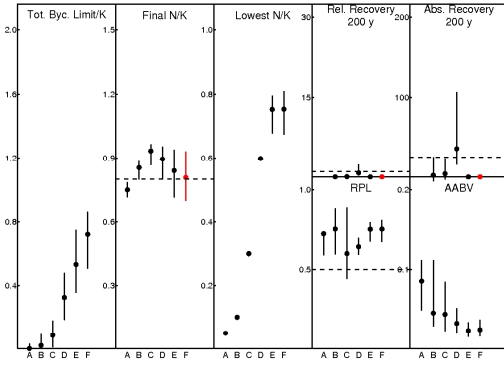


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, z = 13.5, rmax = 2%)

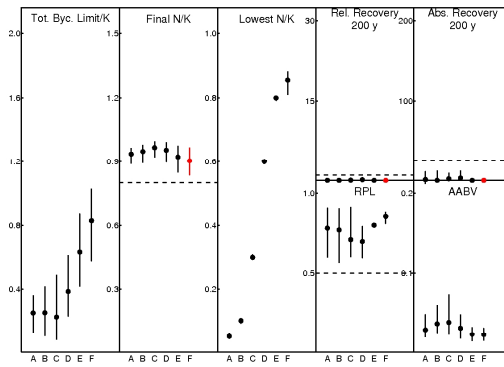


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(PBR3IWCDep, z = 13.5, rmax = 4%)

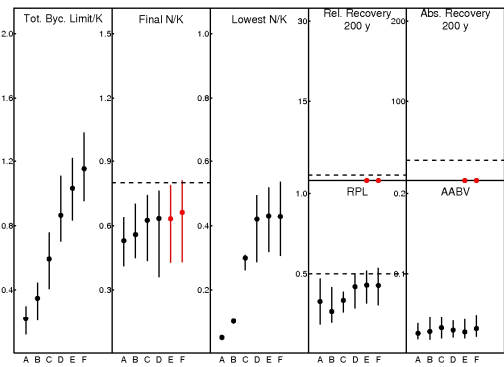




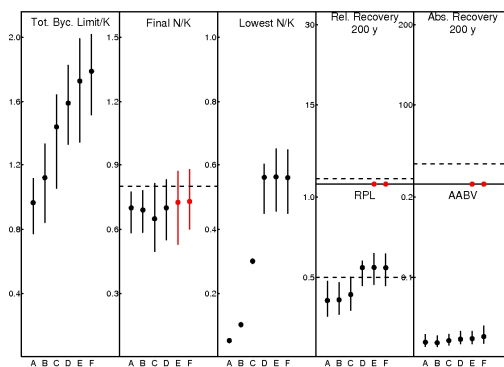
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, BiasSrvyAbs = 0.5, rmax = 2%)



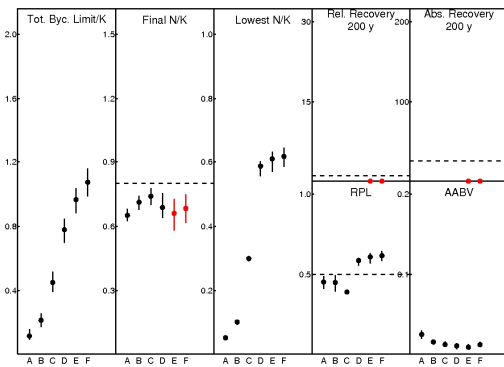
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, BiasSrvyAbs = 0.5, rmax = 4%)



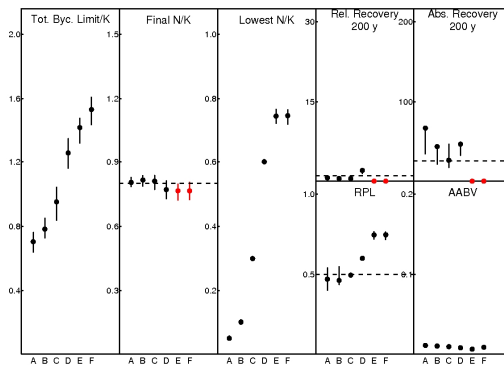
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, BiasSrvyAbs = 1.5, rmax = 2%)



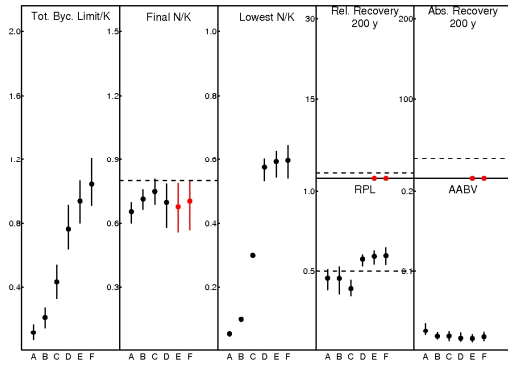
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, BiasSrvyAbs = 1.5, rmax = 4%)



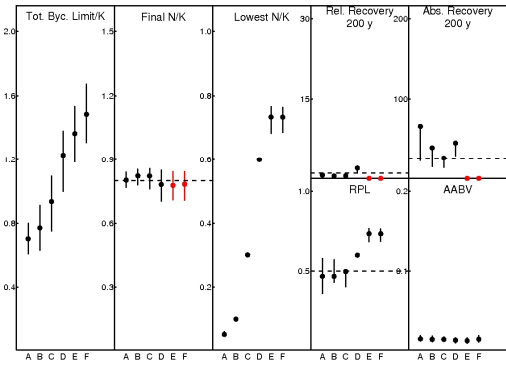
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, BiasSrvyCVAbs = 0.5, rmax = 2%)



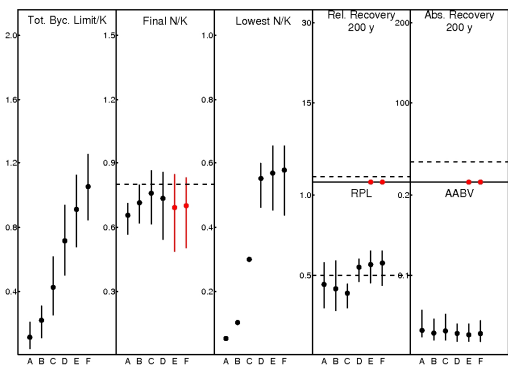
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, BiasSrvyCVAbs = 0.5, rmax = 4%)



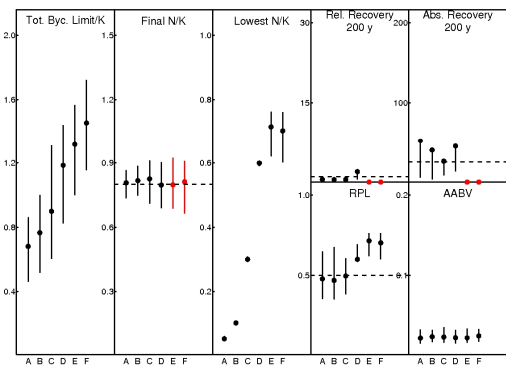
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, BiasSrvyCVAbs = 1, rmax = 2%)



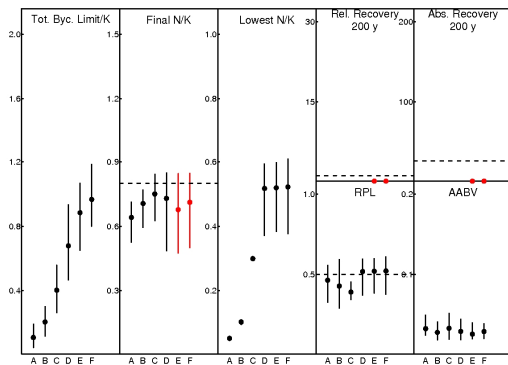
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, BiasSrvyCVAbs = 1, rmax = 4%)



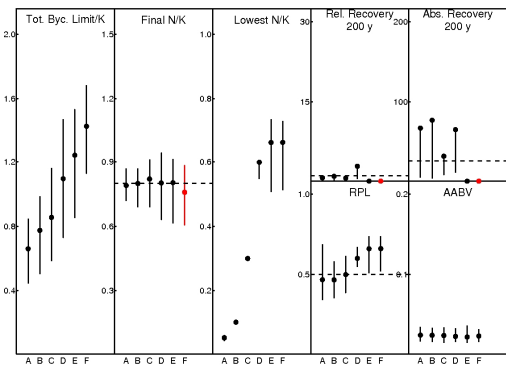
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, BycCV = 0.1, rmax = 2%)



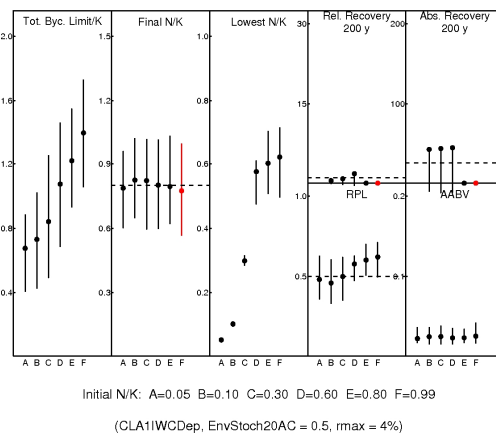
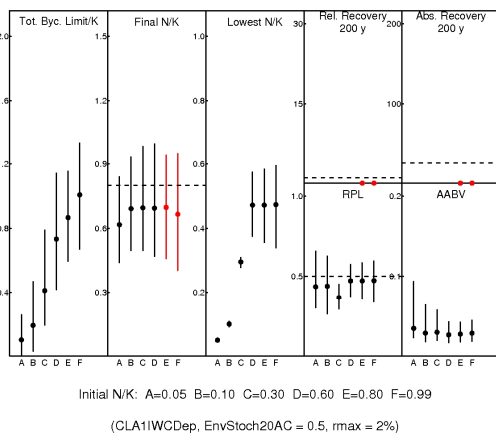
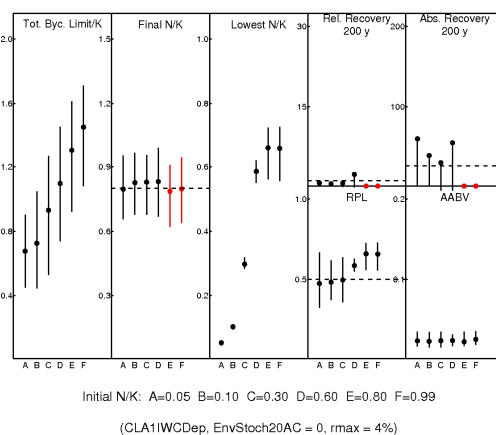
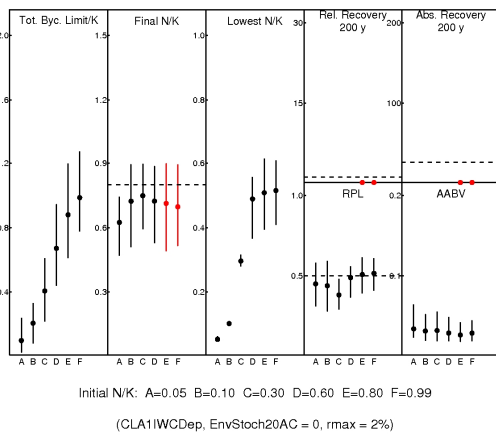
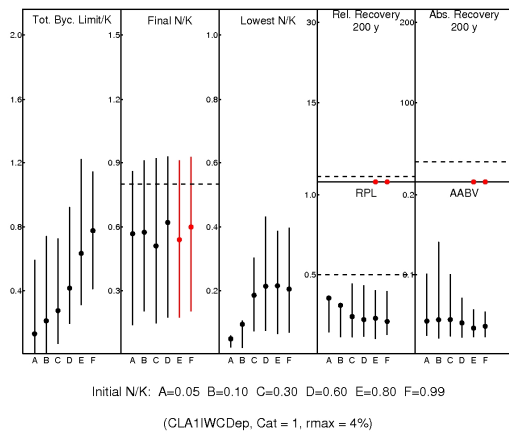
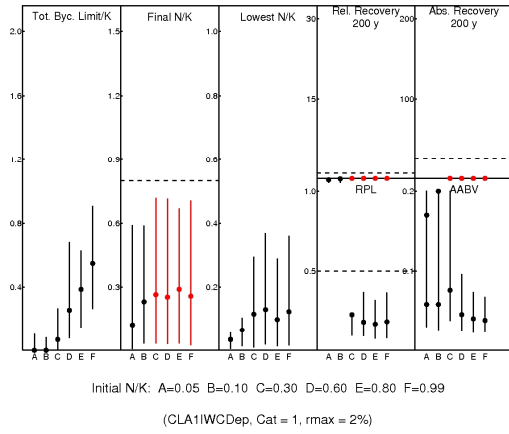
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, BycCV = 0.1, rmax = 4%)

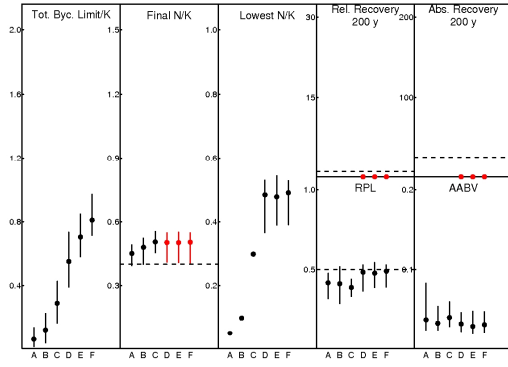


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, BycCV = 1, rmax = 2%)

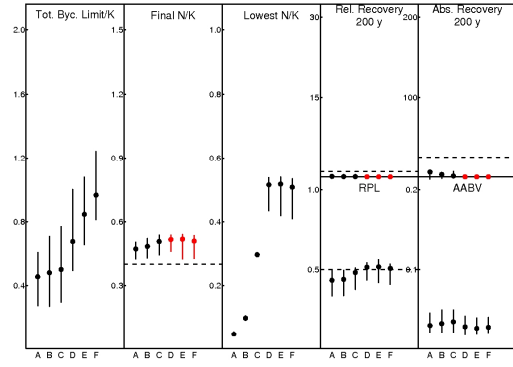


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, BycCV = 1, rmax = 4%)

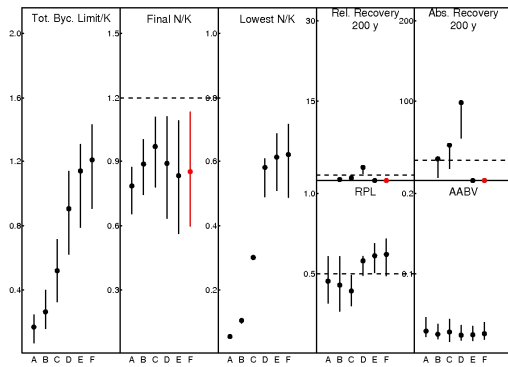




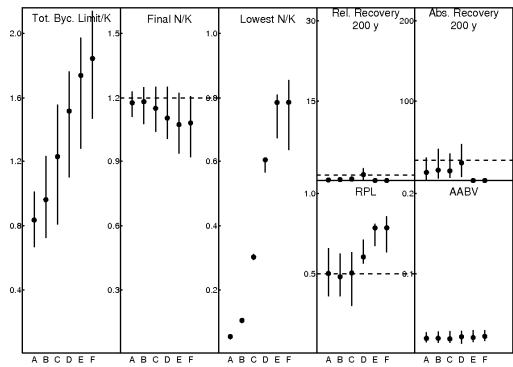
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL11WCDep, KChange = 0.5, rmax = 2%)



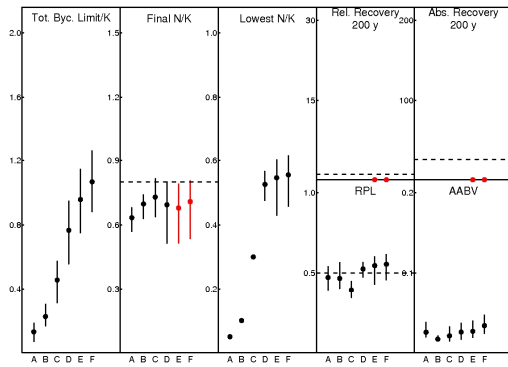
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL11WCDep, KChange = 0.5, rmax = 4%)



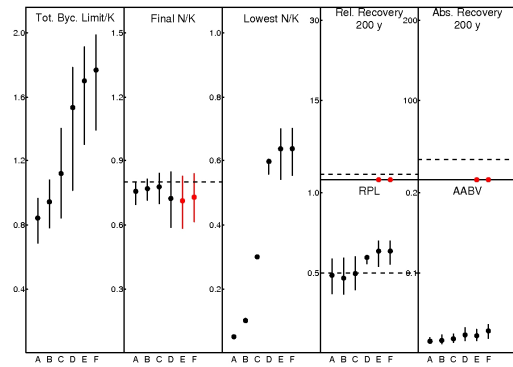
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL11WCDep, KChange = 1.5, rmax = 2%)



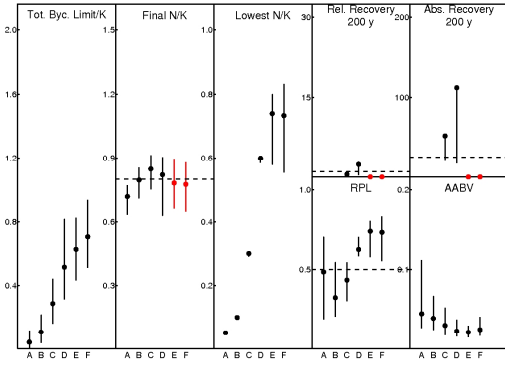
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL11WCDep, KChange = 1.5, rmax = 4%)



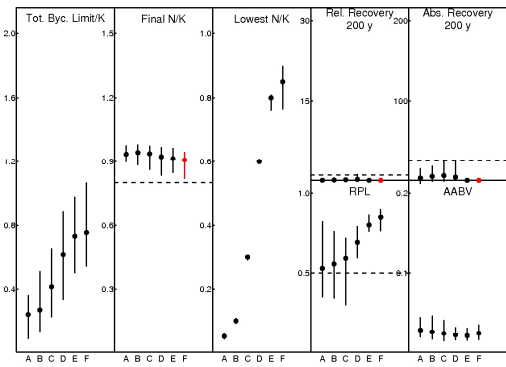
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL11WCDep, SrvyCVAbs = 0.1, rmax = 2%)



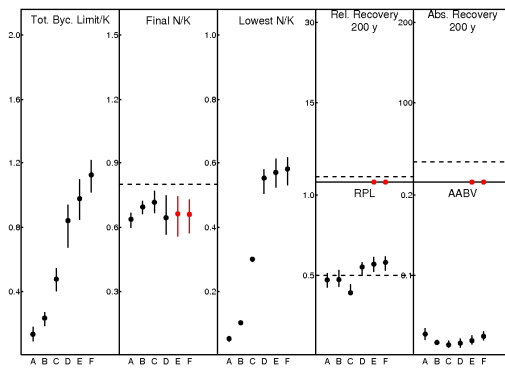
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL11WCDep, SrvyCVAbs = 0.1, rmax = 4%)



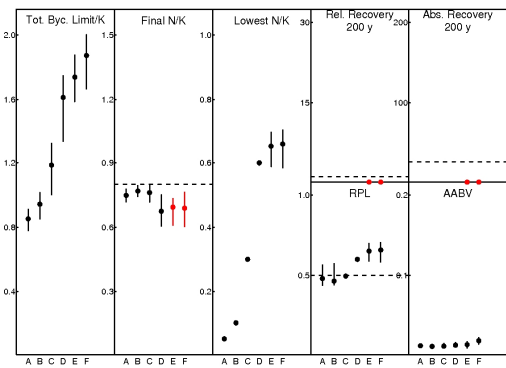
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, SrvyCVAbs = 0.6, rmax = 2%)



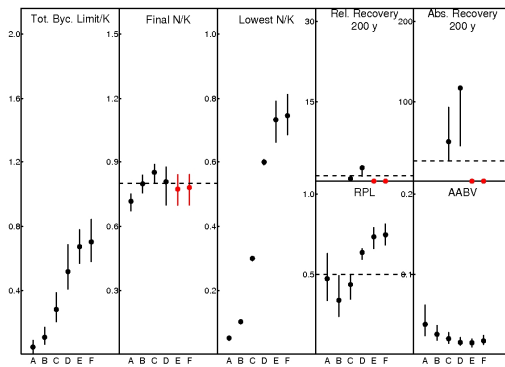
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, SrvyCVAbs = 0.6, rmax = 4%)



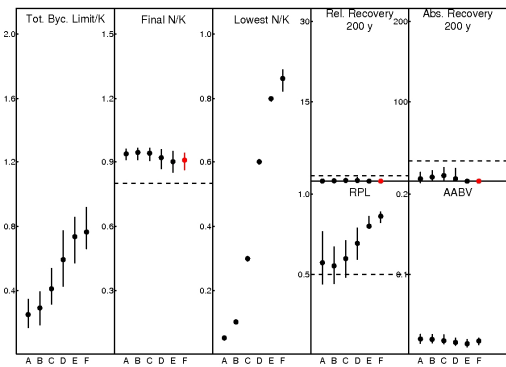
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, SrvyCVAbsUnbias = 0.1, rmax = 2%)



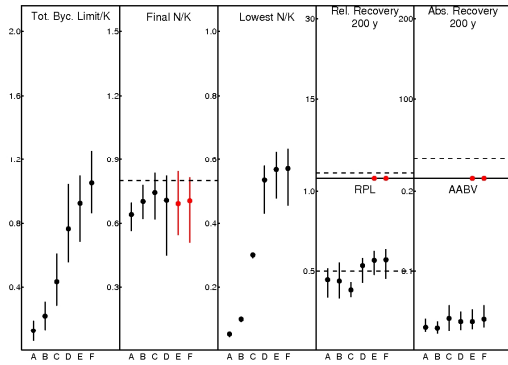
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, SrvyCVAbsUnbias = 0.1, rmax = 4%)



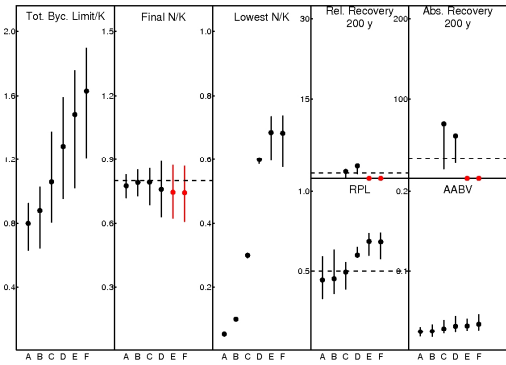
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, SrvyCVAbsUnbias = 0.6, rmax = 2%)



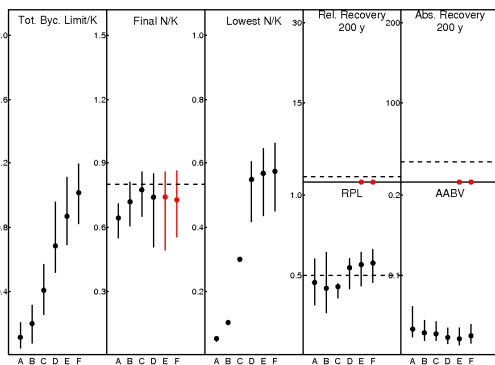
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, SrvyCVAbsUnbias = 0.6, rmax = 4%)



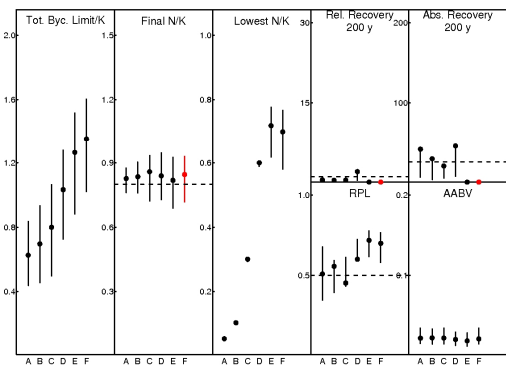
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, SrvyFreq = 5, rmax = 2%)



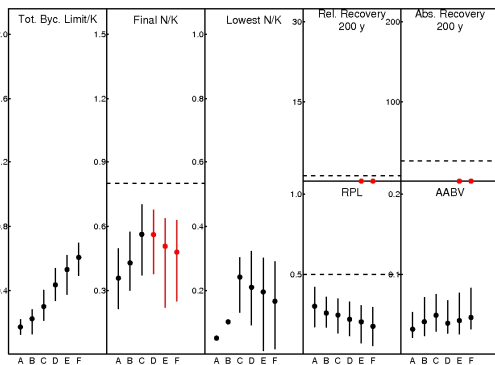
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, SrvyFreq = 5, rmax = 4%)



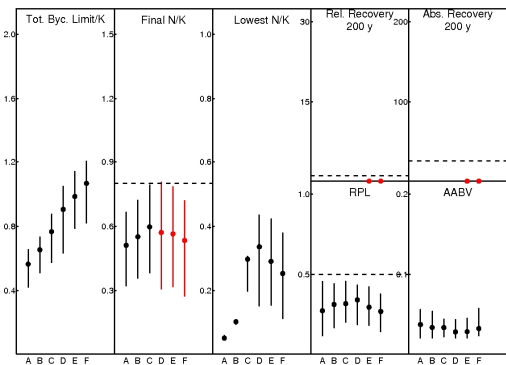
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, SrvyFreq = 15, rmax = 2%)



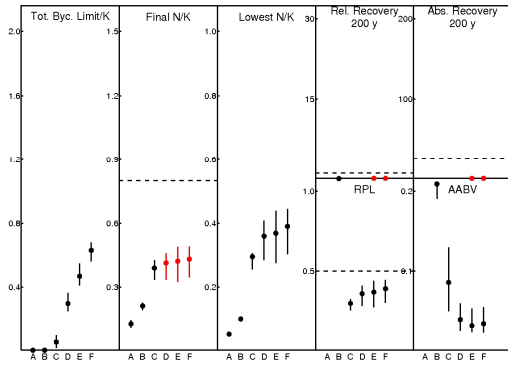
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, SrvyFreq = 15, rmax = 4%)



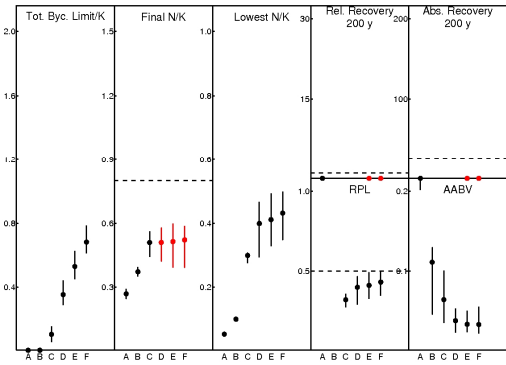
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, WorstCase = 1, rmax = 2%)



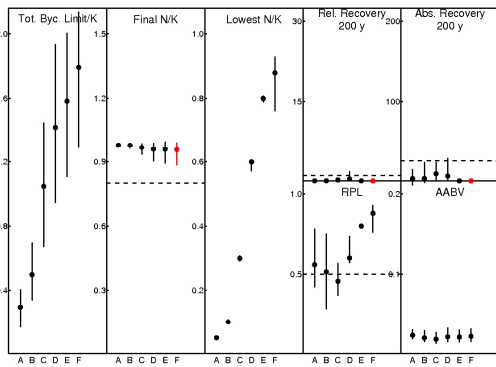
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, WorstCase = 1, rmax = 4%)



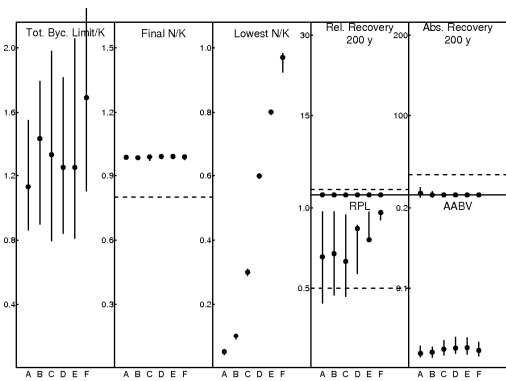
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, z = 0.1, rmax = 2%)



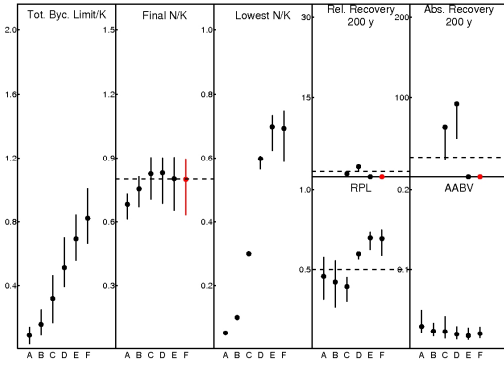
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, z = 0.1, rmax = 4%)



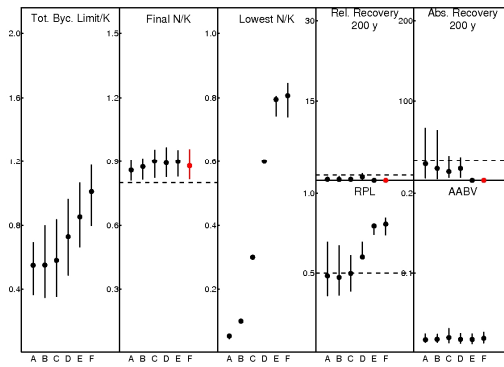
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, z = 13.5, rmax = 2%)



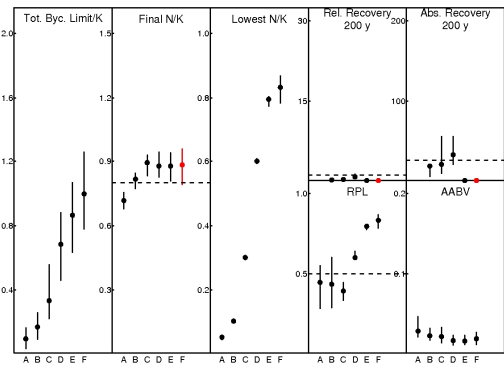
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA1IWCDep, z = 13.5, rmax = 4%)



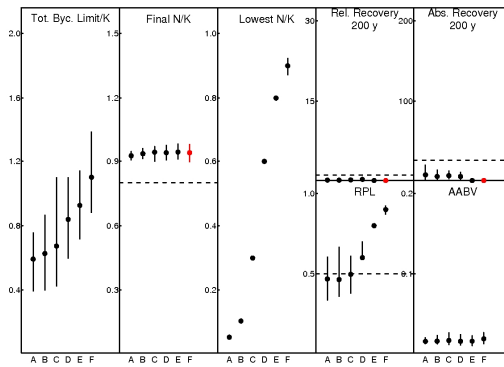
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(CLA2IWCDep, Base = 1, rmax = 2%)



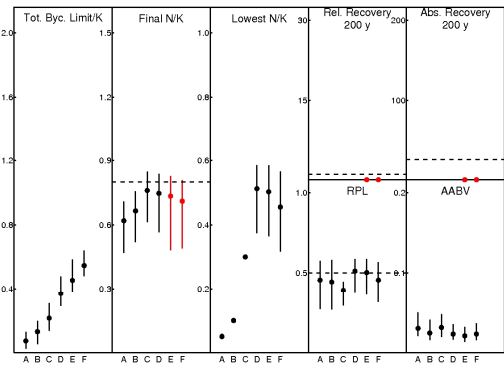
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(CLA2IWCDep, Base = 1, rmax = 4%)



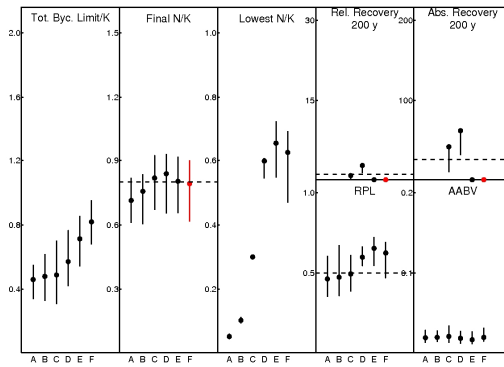
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(CLA2IWCDep, BiasByc = 0.5, rmax = 2%)



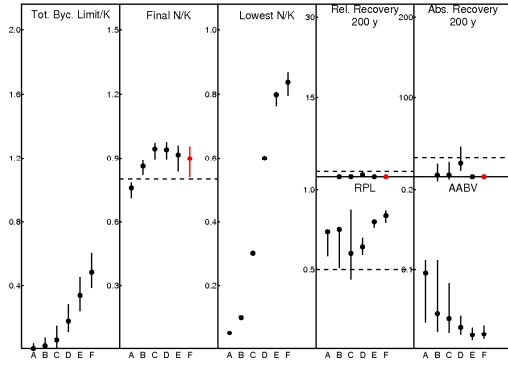
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(CLA2IWCDep, BiasByc = 0.5, rmax = 4%)



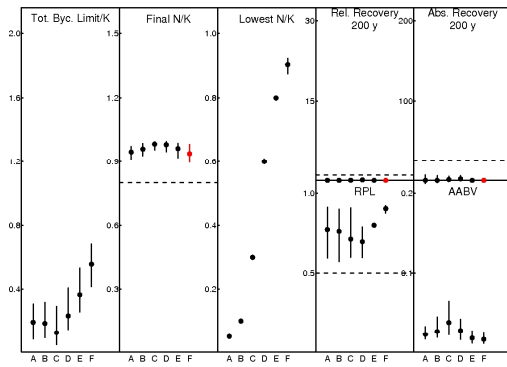
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(CLA2IWCDep, BiasByc = 2, rmax = 2%)



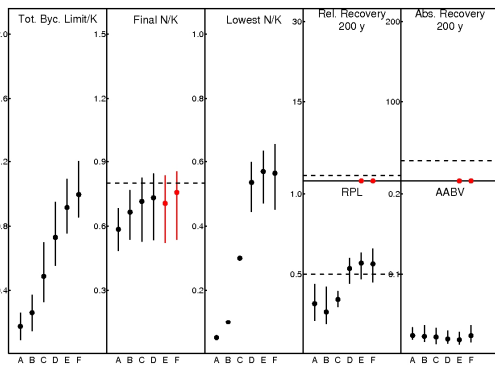
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(CLA2IWCDep, BiasByc = 2, rmax = 4%)



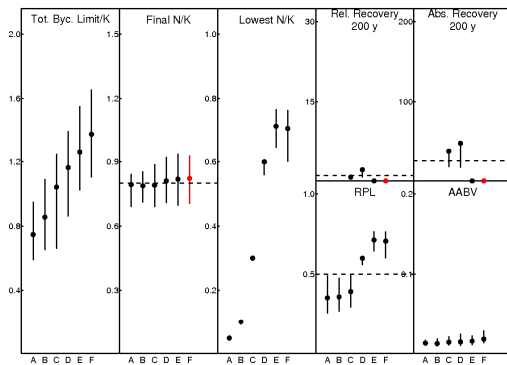
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2IWCDep, BiasSrvyAbs = 0.5, rmax = 2%)



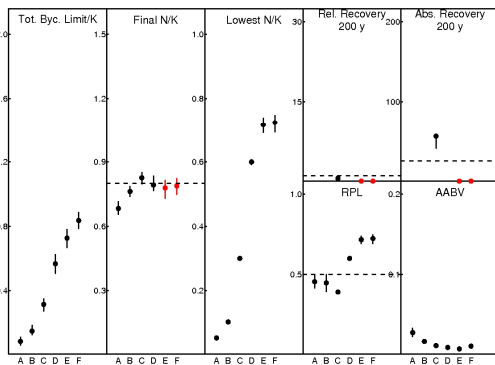
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2IWCDep, BiasSrvyAbs = 0.5, rmax = 4%)



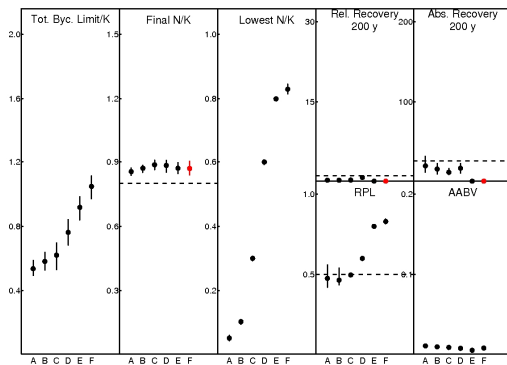
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2IWCDep, BiasSrvyAbs = 1.5, rmax = 2%)



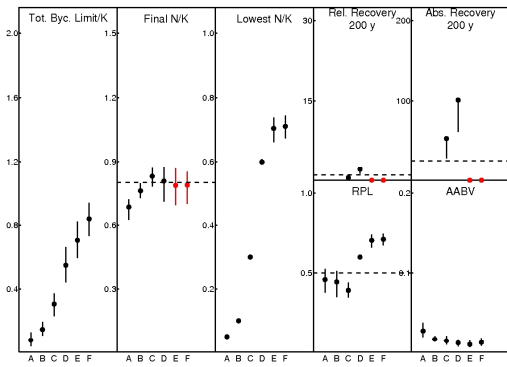
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2IWCDep, BiasSrvyAbs = 1.5, rmax = 4%)



Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2IWCDep, BiasSrvyCVAbs = 0.5, rmax = 2%)

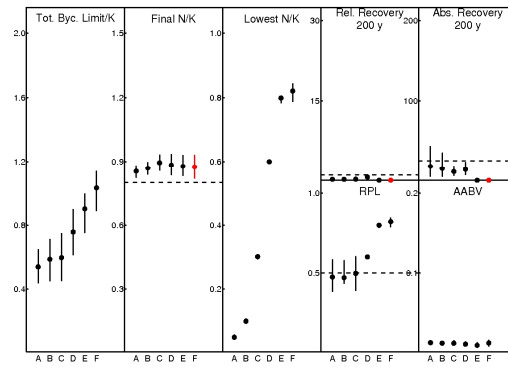


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2IWCDep, BiasSrvyCVAbs = 0.5, rmax = 4%)



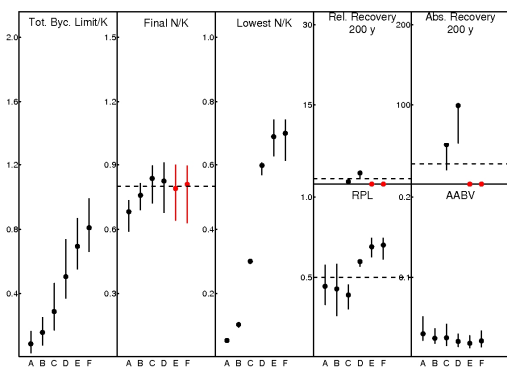
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99

(CLA2IWCDep, BiasSrvyCVAbs = 1, rmax = 2%)



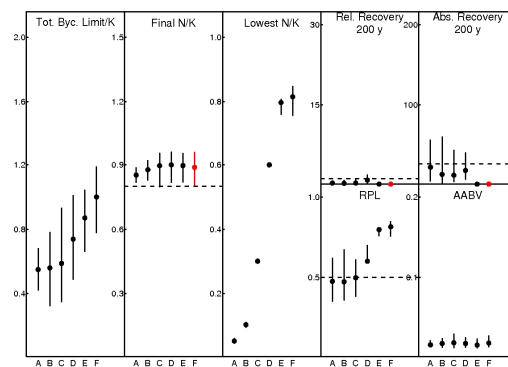
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99

(CLA2IWCDep, BiasSrvyCVAbs = 1, rmax = 4%)



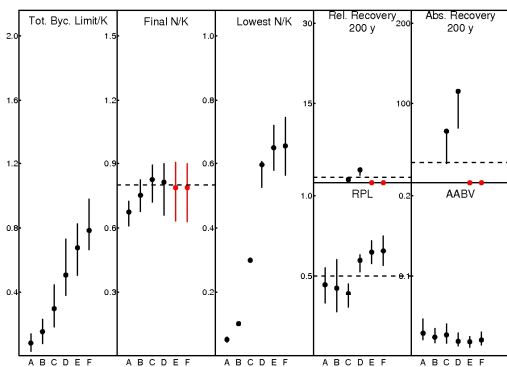
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99

(CLA2IWCDep, BycCV = 0.1, rmax = 2%)



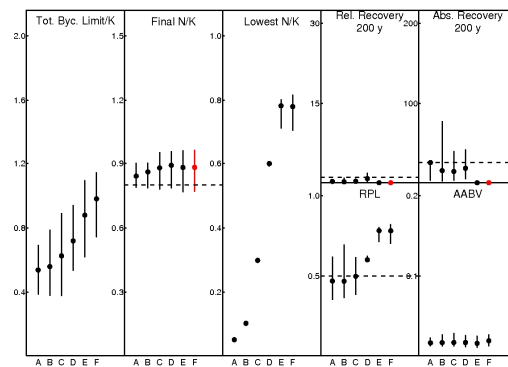
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99

(CLA2IWCDep, BycCV = 0.1, rmax = 4%)



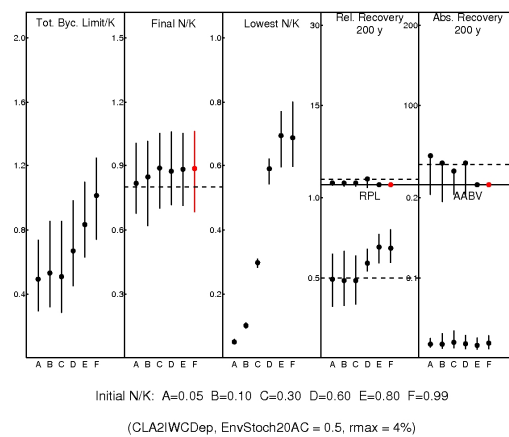
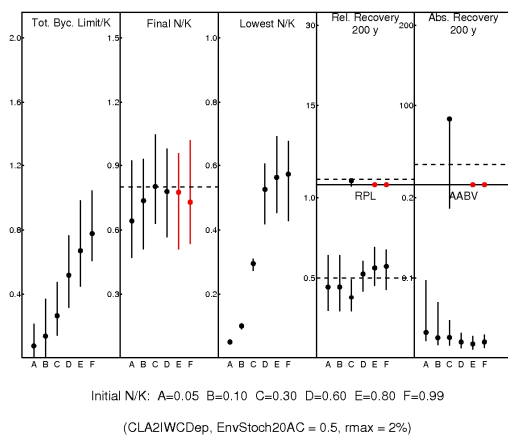
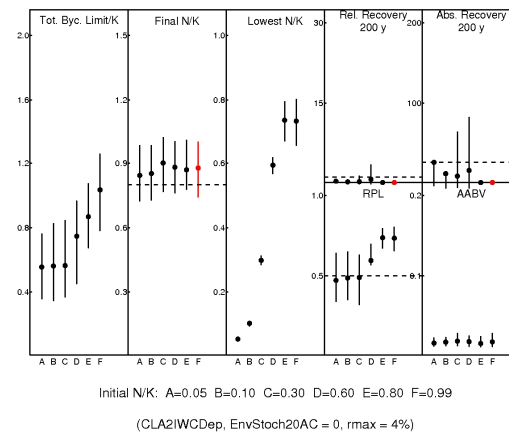
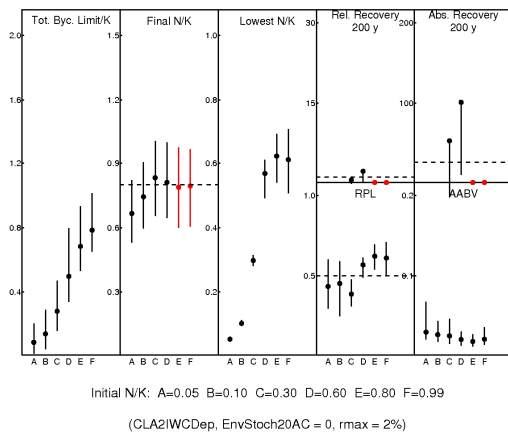
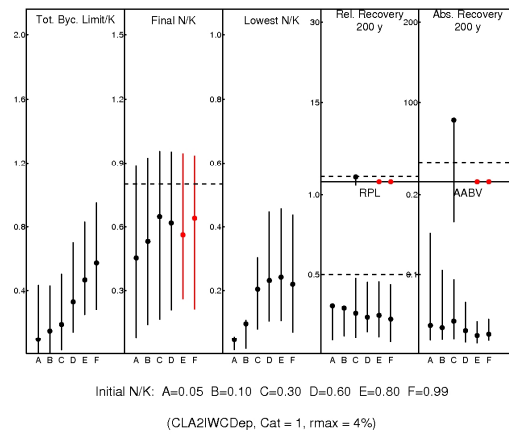
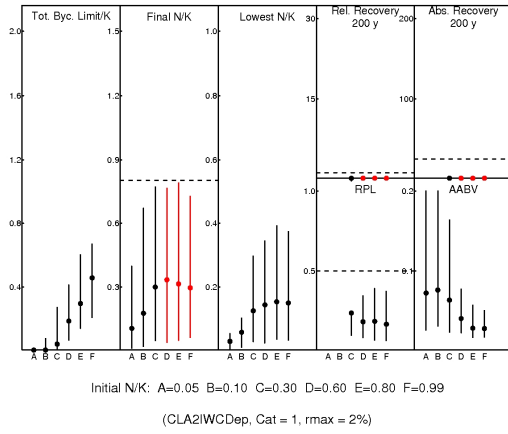
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99

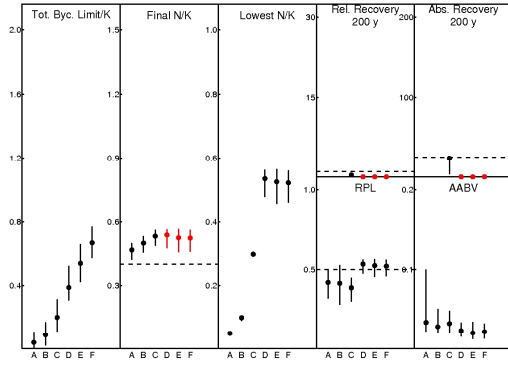
(CLA2IWCDep, BycCV = 1, rmax = 2%)



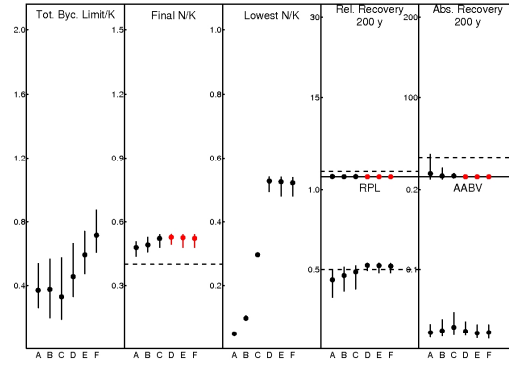
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99

(CLA2IWCDep, BycCV = 1, rmax = 4%)

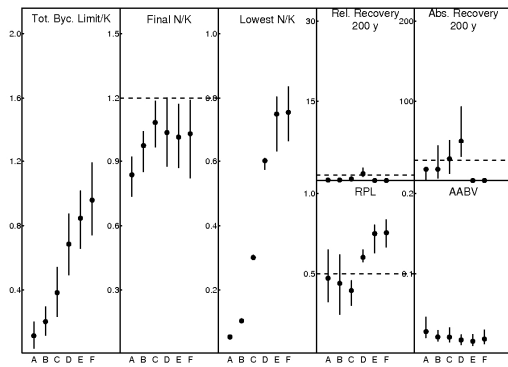




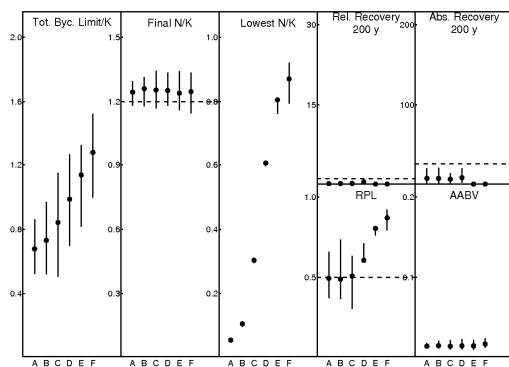
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2)WCDep, KChange = 0.5, rmax = 2%



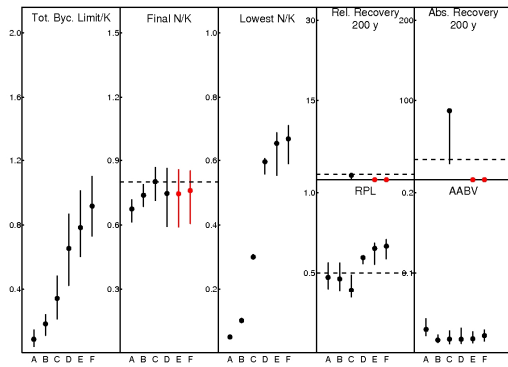
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2)WCDep, KChange = 0.5, rmax = 4%



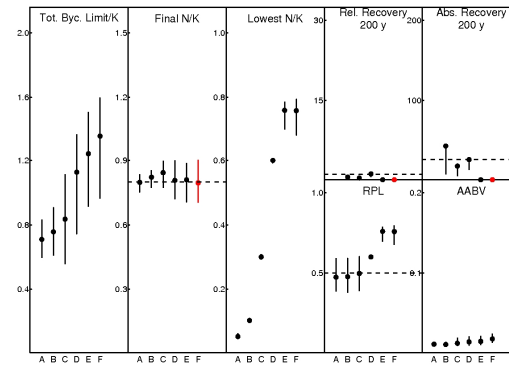
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2)WCDep, KChange = 1.5, rmax = 2%



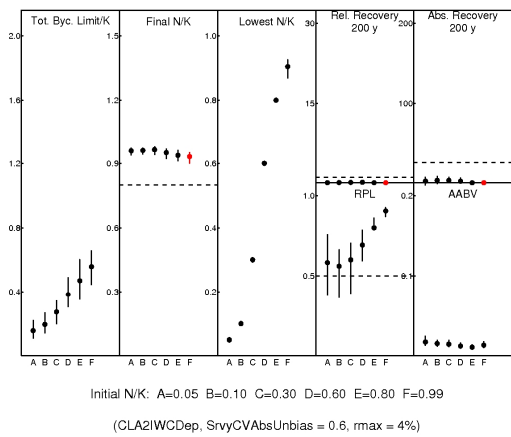
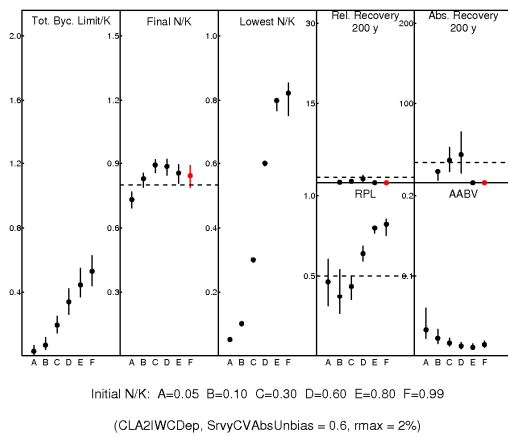
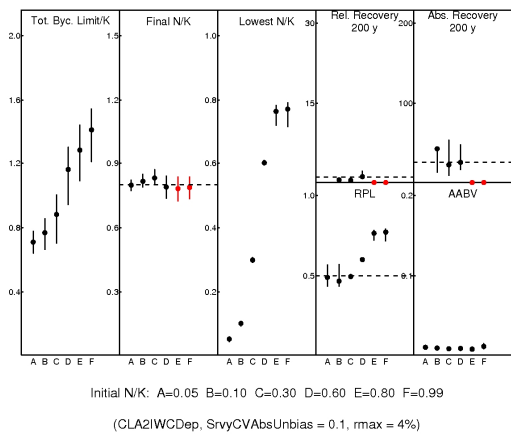
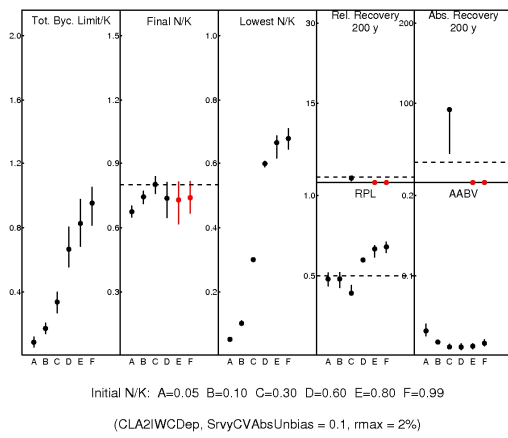
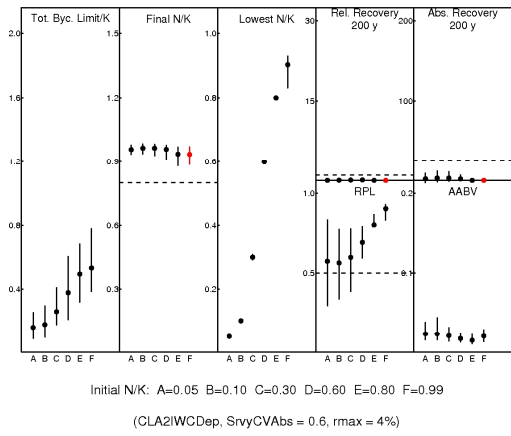
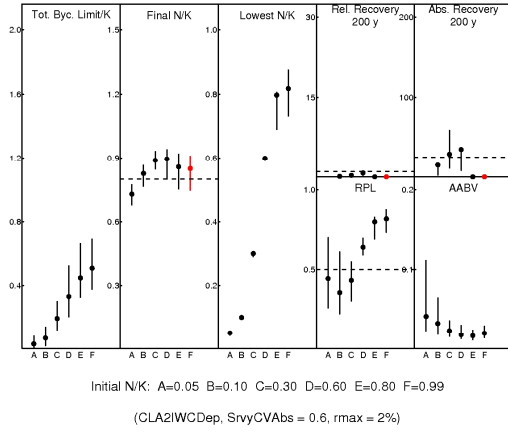
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2)WCDep, KChange = 1.5, rmax = 4%

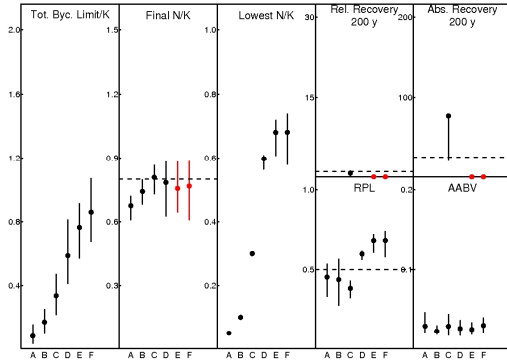


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2)WCDep, SrvyCVAbs = 0.1, rmax = 2%

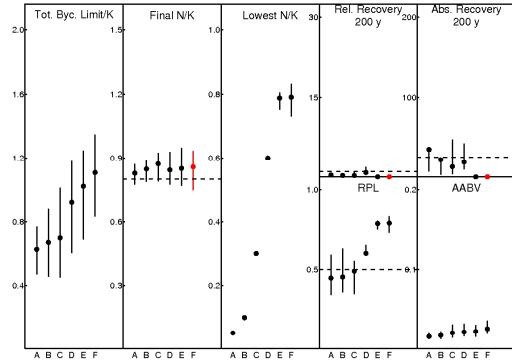


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2)WCDep, SrvyCVAbs = 0.1, rmax = 4%

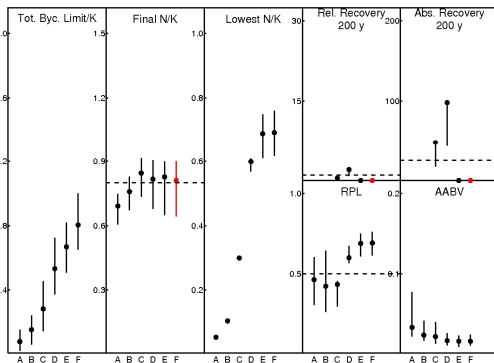




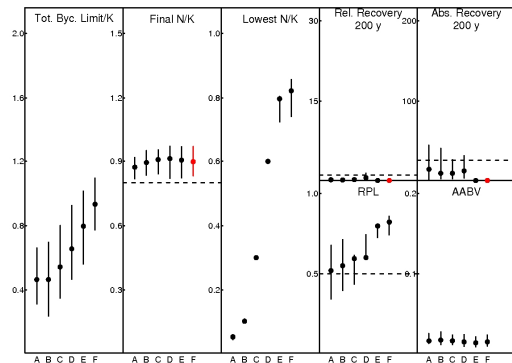
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2)WCDep, SrvyFreq = 5, rmax = 2%



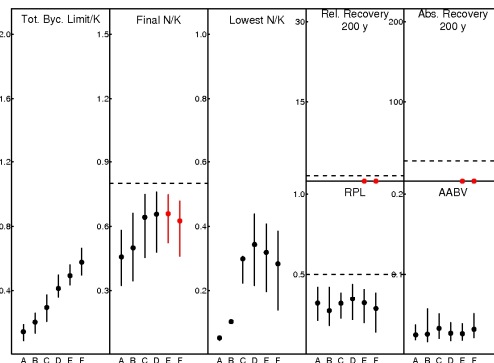
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2)WCDep, SrvyFreq = 5, rmax = 4%



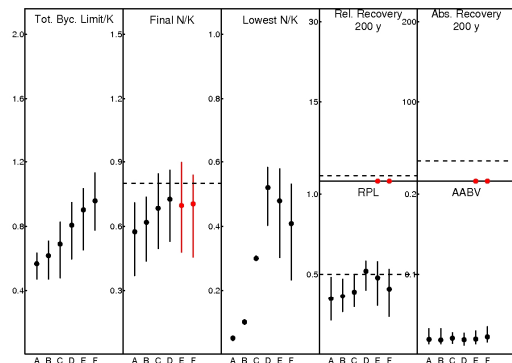
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2)WCDep, SrvyFreq = 15, rmax = 2%



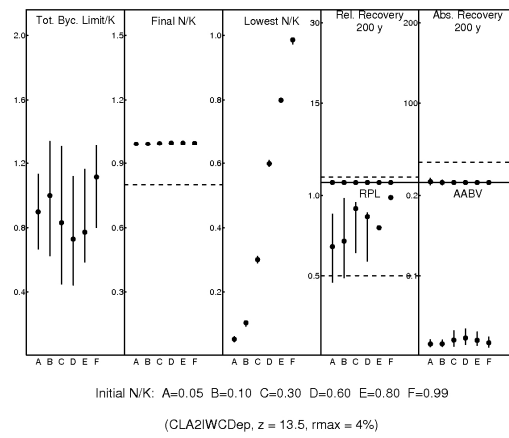
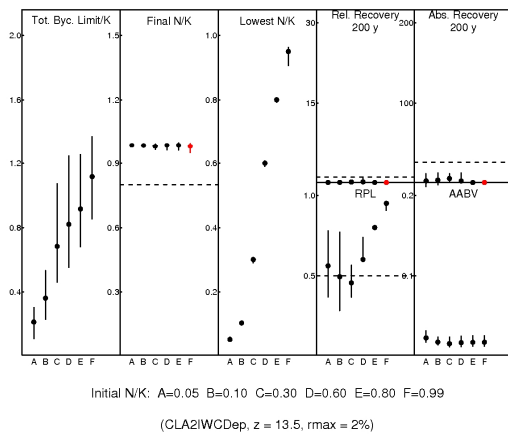
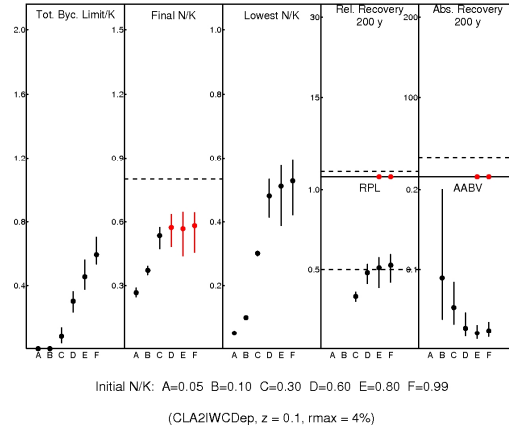
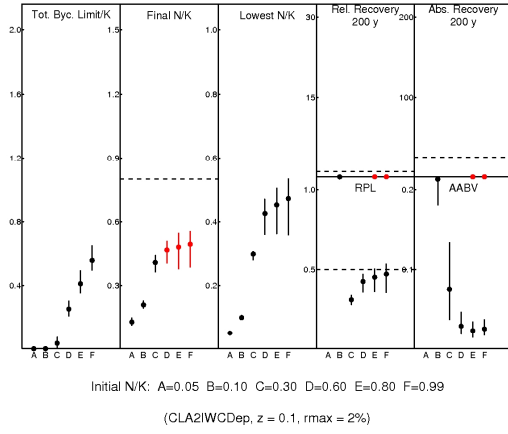
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2)WCDep, SrvyFreq = 15, rmax = 4%

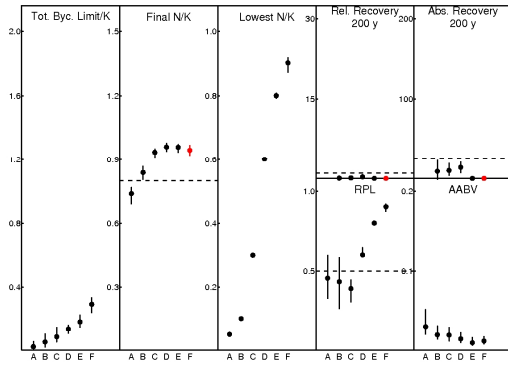


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2)WCDep, WorstCase = 1, rmax = 2%

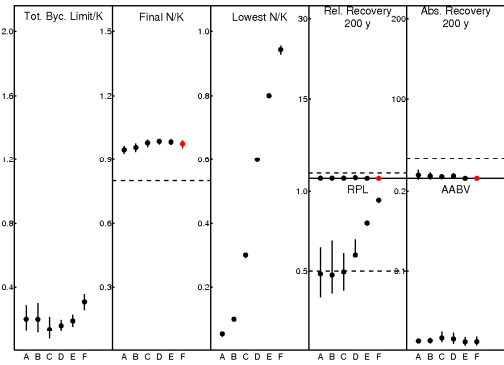


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA2)WCDep, WorstCase = 1, rmax = 4%

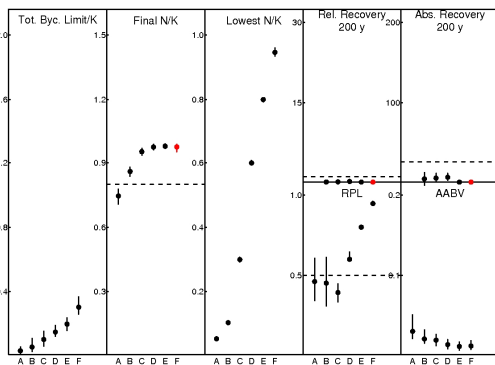




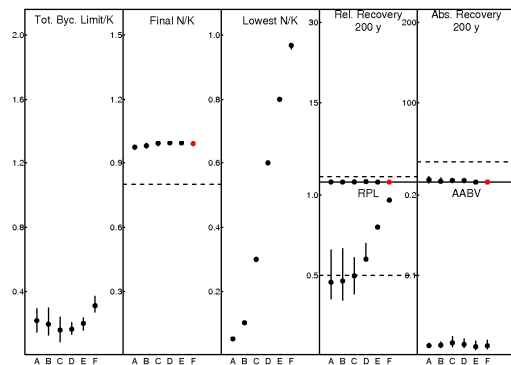
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL3IWCDep, Base = 1, rmax = 2%)



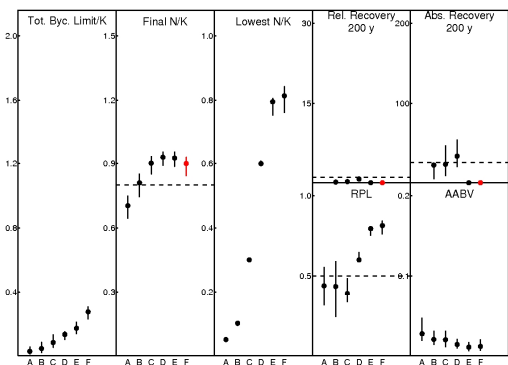
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL3IWCDep, Base = 1, rmax = 4%)



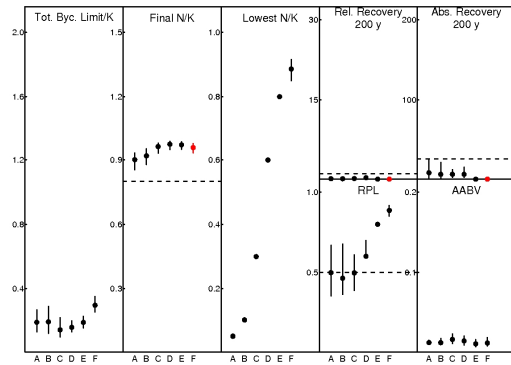
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL3IWCDep, BiasByc = 0.5, rmax = 2%)



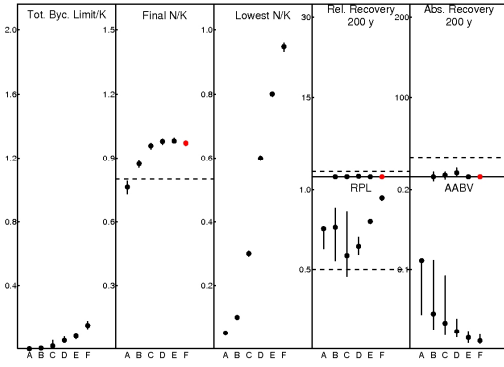
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL3IWCDep, BiasByc = 0.5, rmax = 4%)



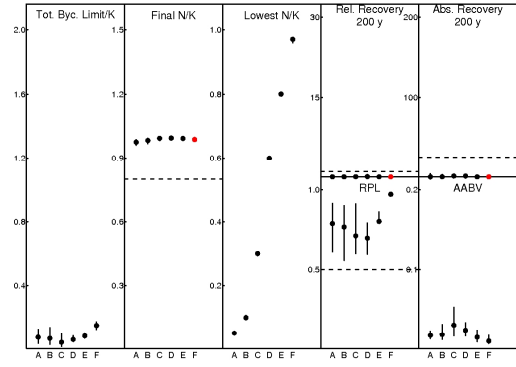
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL3IWCDep, BiasByc = 2, rmax = 2%)



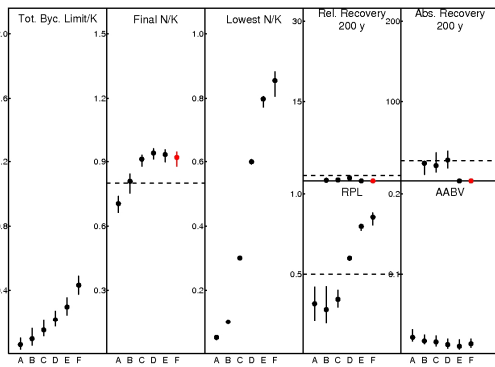
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL3IWCDep, BiasByc = 2, rmax = 4%)



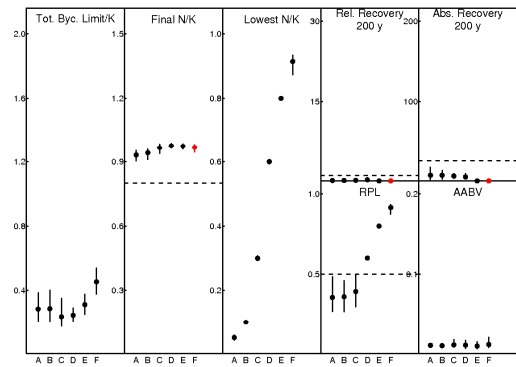
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(CLA3IWCDep, BiasSrvyAbs = 0.5, rmax = 2%)



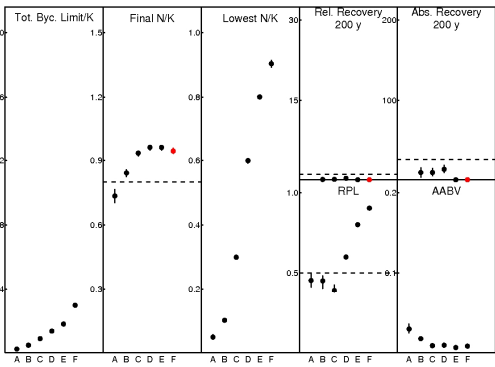
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(CLA3IWCDep, BiasSrvyAbs = 0.5, rmax = 4%)



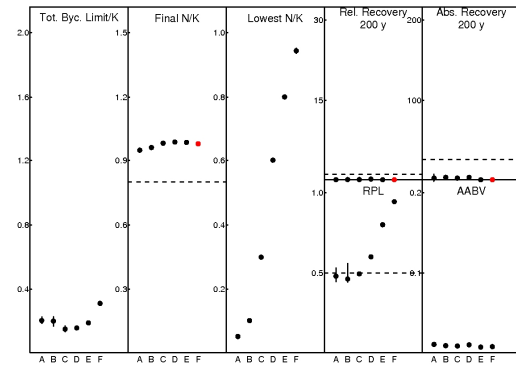
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(CLA3IWCDep, BiasSrvyAbs = 1.5, rmax = 2%)



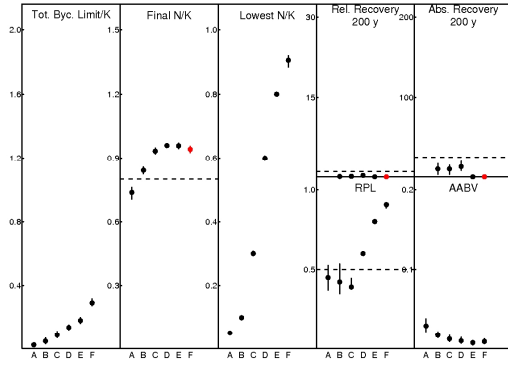
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(CLA3IWCDep, BiasSrvyAbs = 1.5, rmax = 4%)



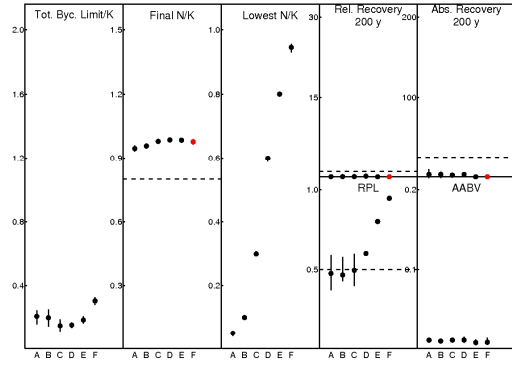
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(CLA3IWCDep, BiasSrvyCVAbs = 0.5, rmax = 2%)



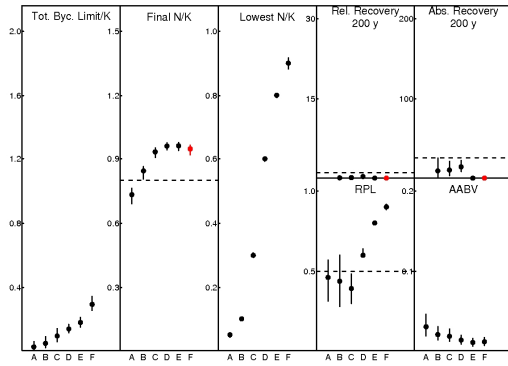
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
(CLA3IWCDep, BiasSrvyCVAbs = 0.5, rmax = 4%)



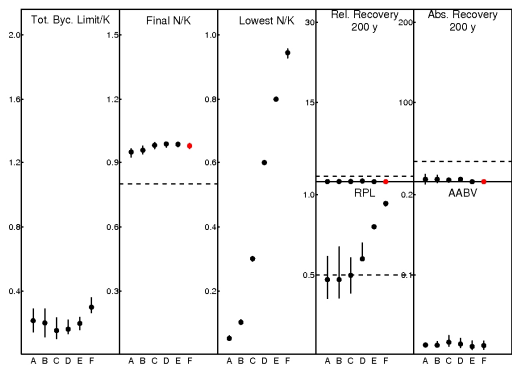
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA3IWCDep, BiasSrvyCVAbs = 1, rmax = 2%)



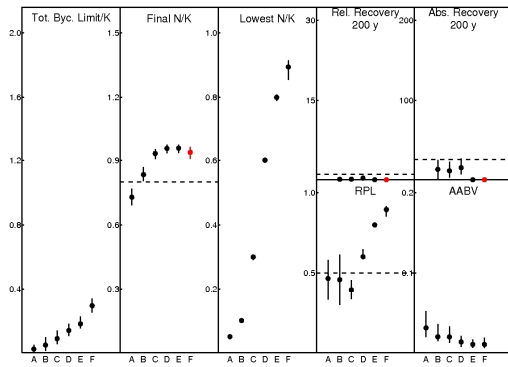
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA3IWCDep, BiasSrvyCVAbs = 1, rmax = 4%)



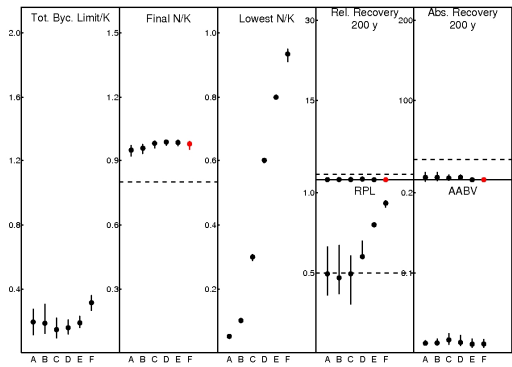
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA3IWCDep, BycCV = 0.1, rmax = 2%)



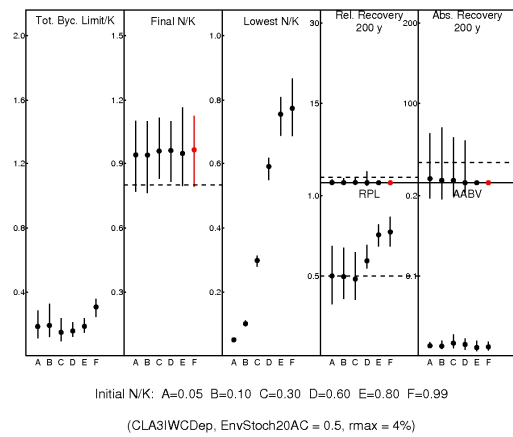
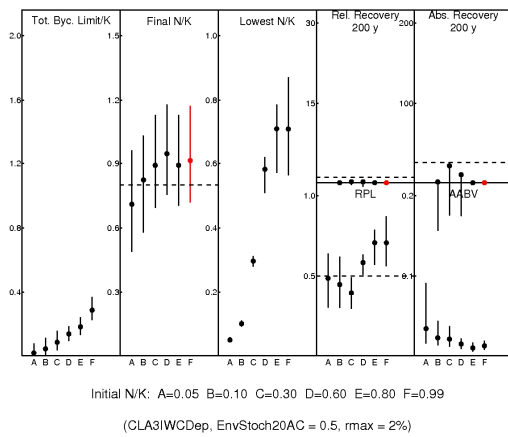
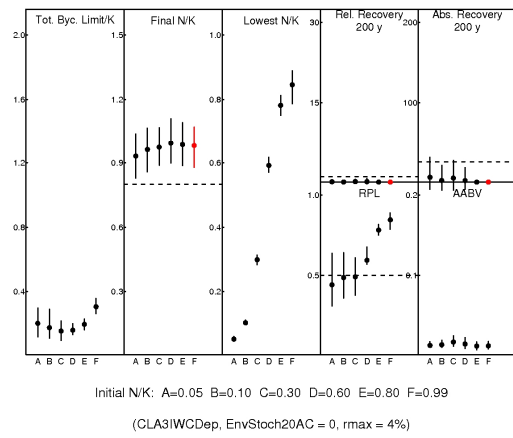
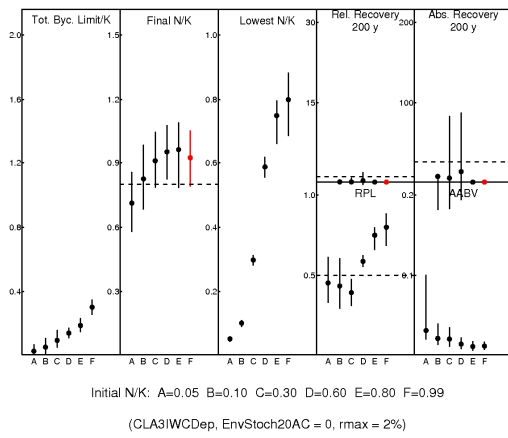
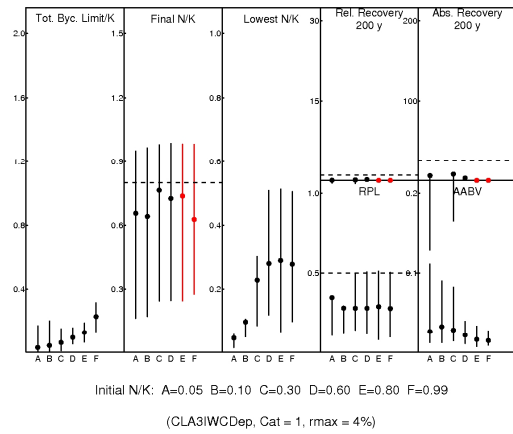
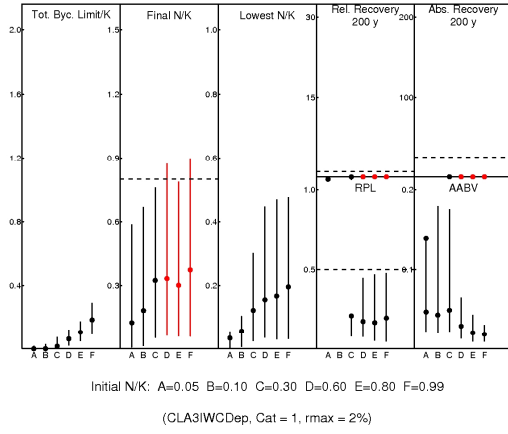
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA3IWCDep, BycCV = 0.1, rmax = 4%)

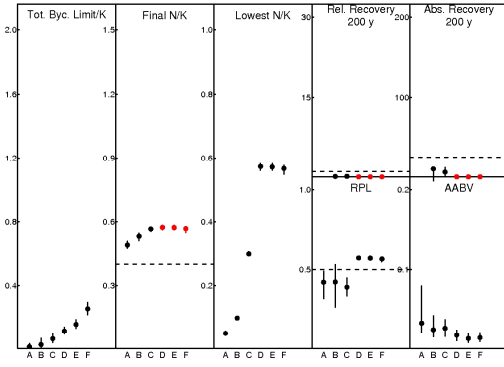


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA3IWCDep, BycCV = 1, rmax = 2%)

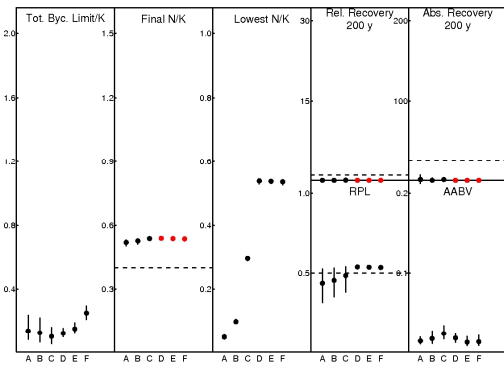


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA3IWCDep, BycCV = 1, rmax = 4%)

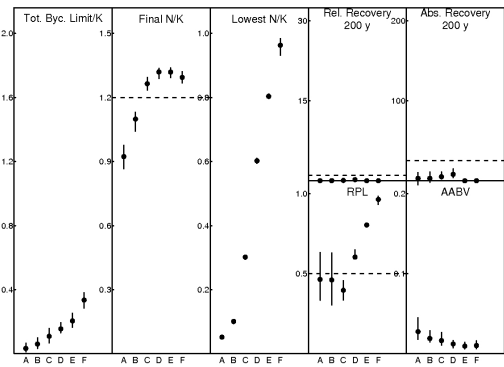




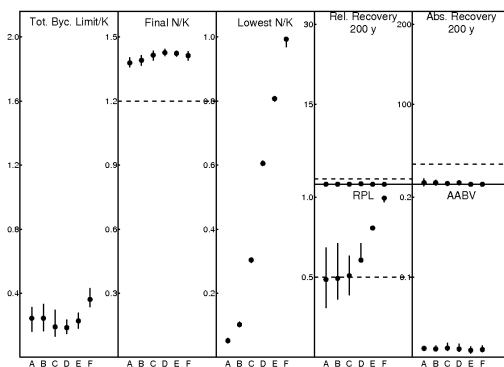
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL3IWCDep, KChange = 0.5, rmax = 2%)



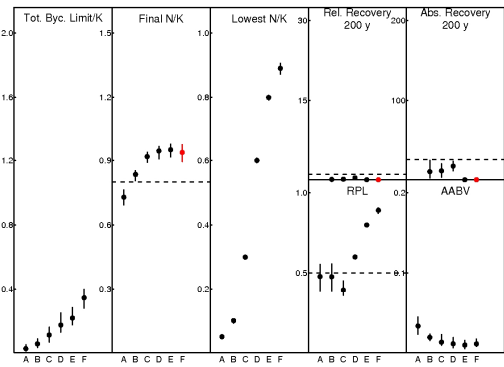
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL3IWCDep, KChange = 0.5, rmax = 4%)



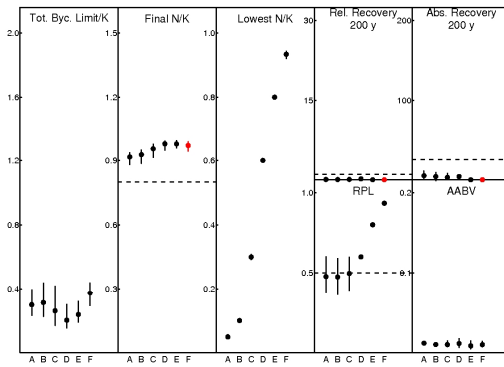
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL3IWCDep, KChange = 1.5, rmax = 2%)



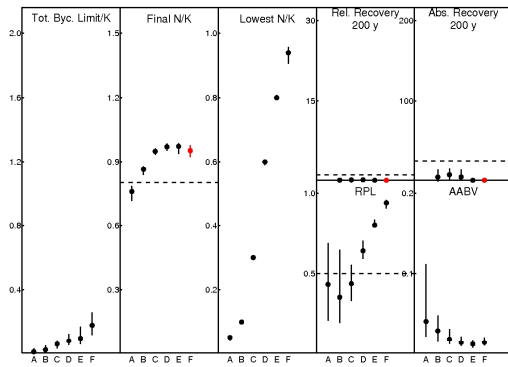
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL3IWCDep, KChange = 1.5, rmax = 4%)



Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL3IWCDep, SrvyCVAbs = 0.1, rmax = 2%)

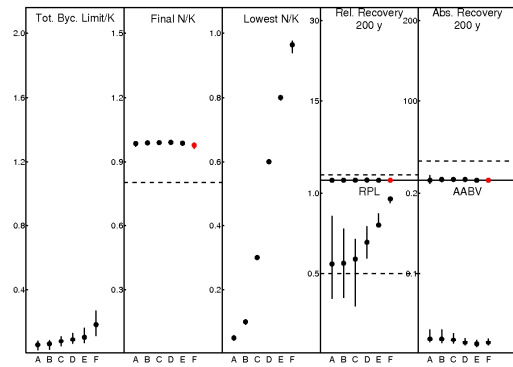


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CL3IWCDep, SrvyCVAbs = 0.1, rmax = 4%)



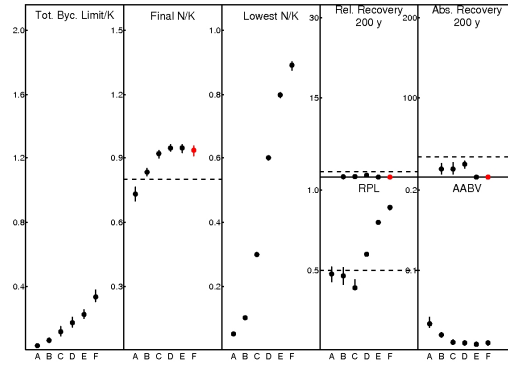
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99

(CLA3IWCDep, SrvyCVAbs = 0.6, rmax = 2%)



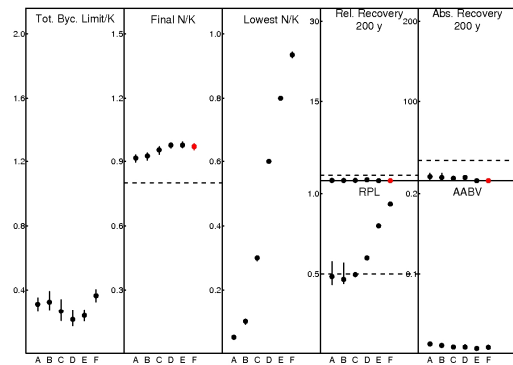
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99

(CLA3IWCDep, SrvyCVAbs = 0.6, rmax = 4%)



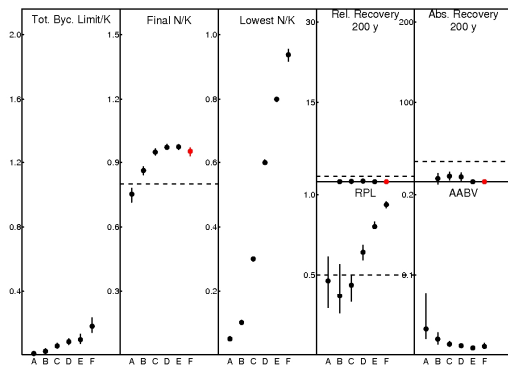
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99

(CLA3IWCDep, SrvyCVAbsUnbias = 0.1, rmax = 2%)



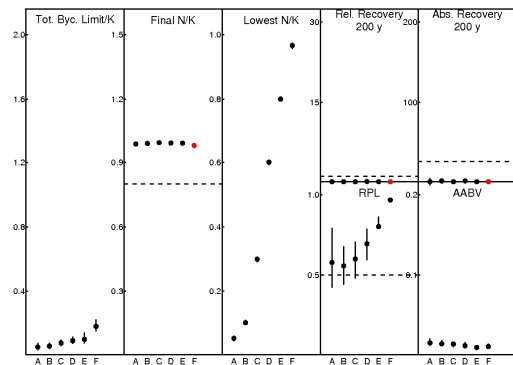
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99

(CLA3IWCDep, SrvyCVAbsUnbias = 0.1, rmax = 4%)



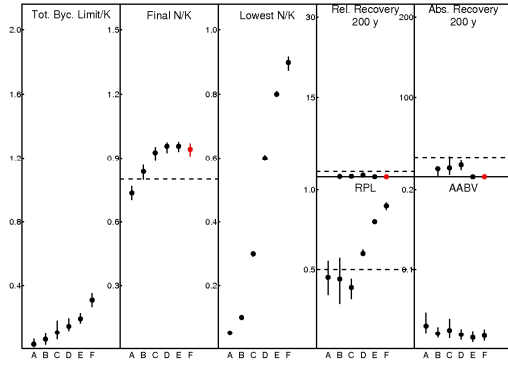
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99

(CLA3IWCDep, SrvyCVAbsUnbias = 0.6, rmax = 2%)

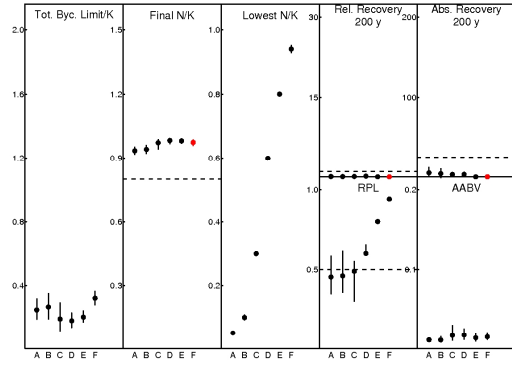


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99

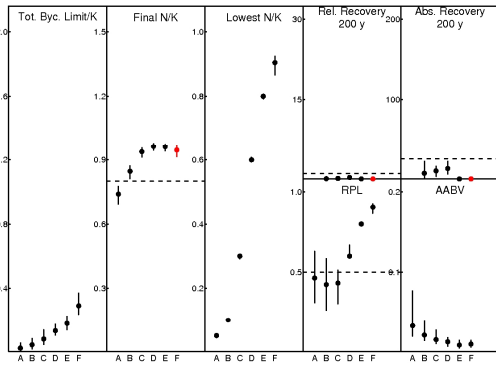
(CLA3IWCDep, SrvyCVAbsUnbias = 0.6, rmax = 4%)



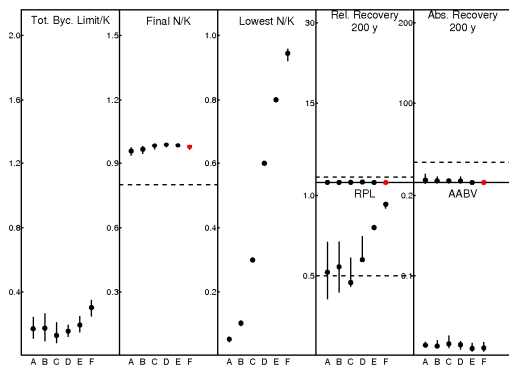
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA3IWCDep, SrvyFreq = 5, rmax = 2%)



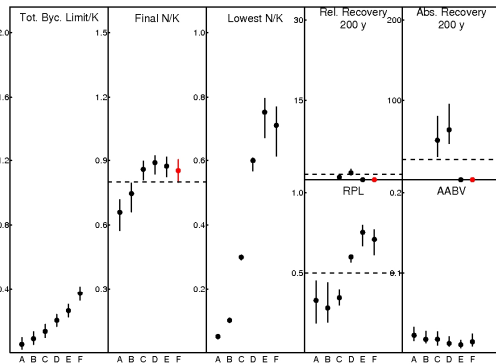
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA3IWCDep, SrvyFreq = 5, rmax = 4%)



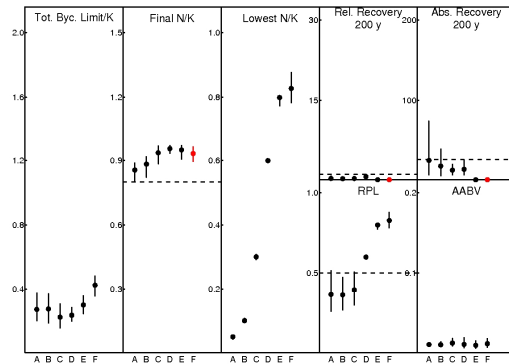
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA3IWCDep, SrvyFreq = 15, rmax = 2%)



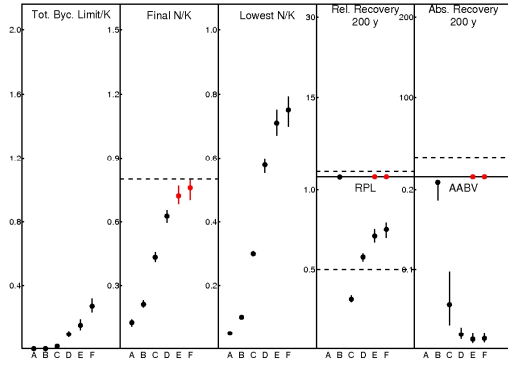
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA3IWCDep, SrvyFreq = 15, rmax = 4%)



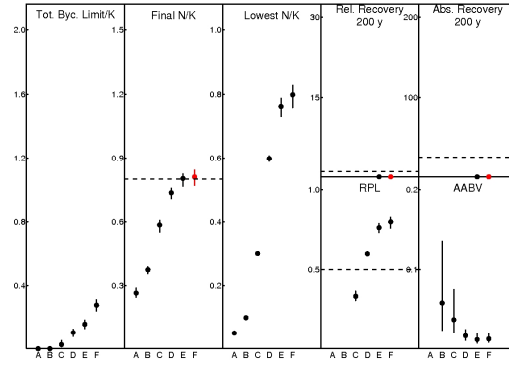
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA3IWCDep, WorstCase = 1, rmax = 2%)



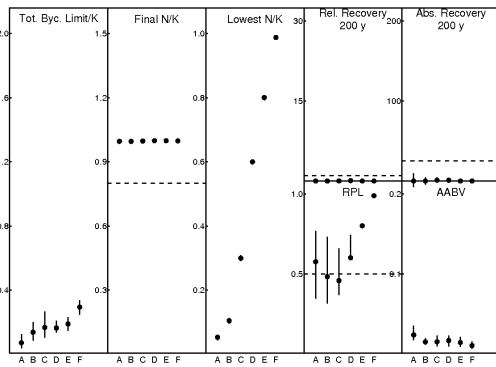
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA3IWCDep, WorstCase = 1, rmax = 4%)



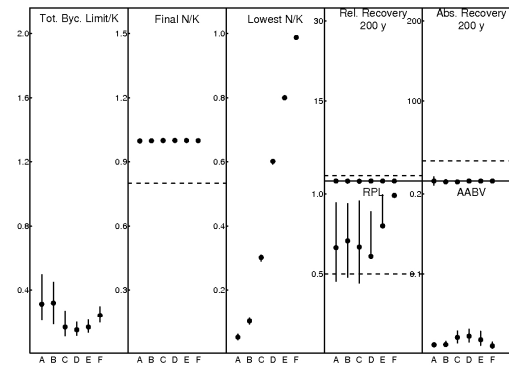
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA3IWCDep, z = 0.1, rmax = 2%)



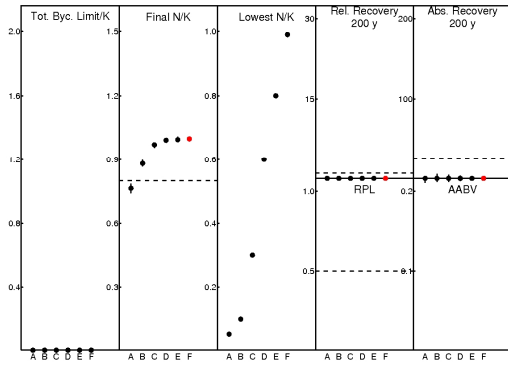
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA3IWCDep, z = 0.1, rmax = 4%)



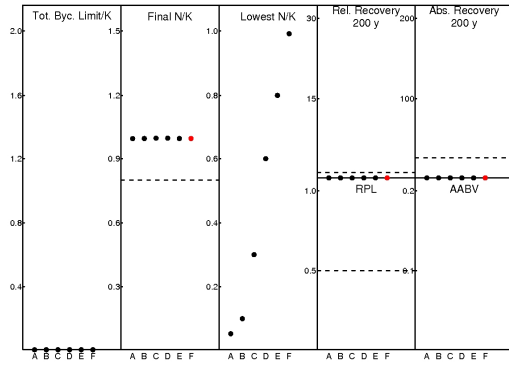
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA3IWCDep, z = 13.5, rmax = 2%)



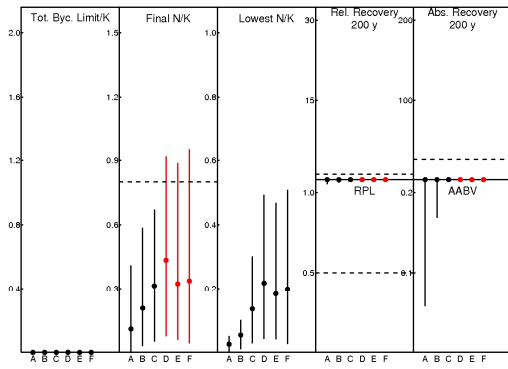
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=0.99
 (CLA3IWCDep, z = 13.5, rmax = 4%)



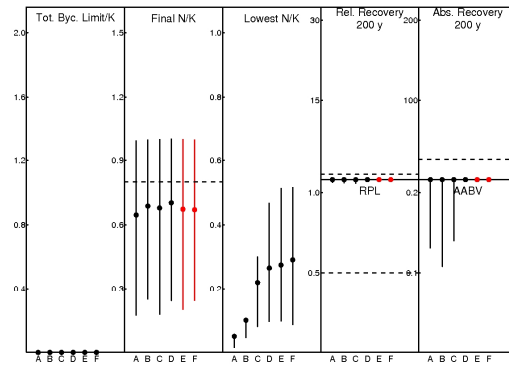
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (NoBycInitDep, Base = 1, rmax = 2%)



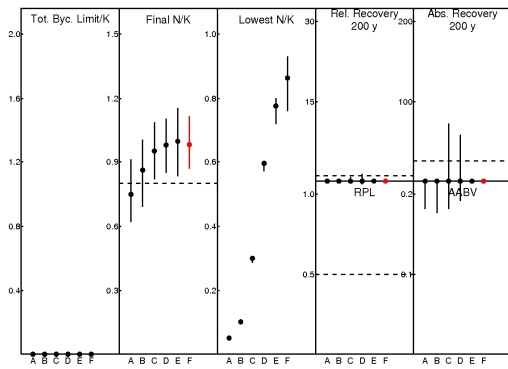
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (NoBycInitDep, Base = 1, rmax = 4%)



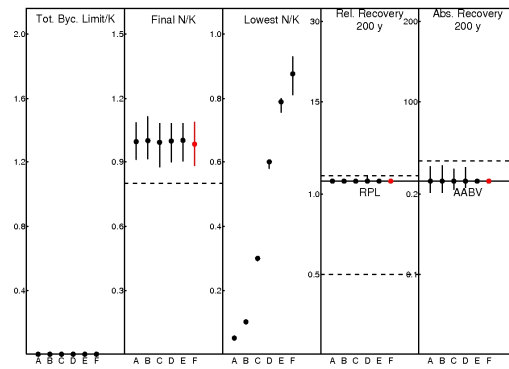
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (NoBycInitDep, Cat = 1, rmax = 2%)



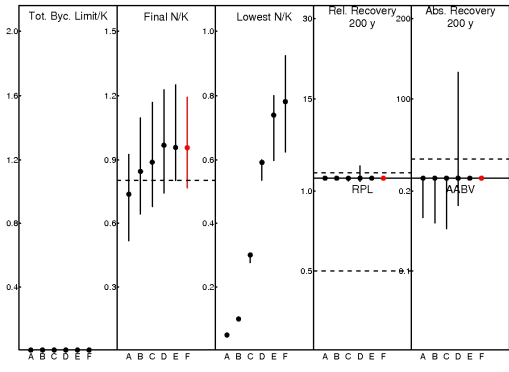
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (NoBycInitDep, Cat = 1, rmax = 4%)



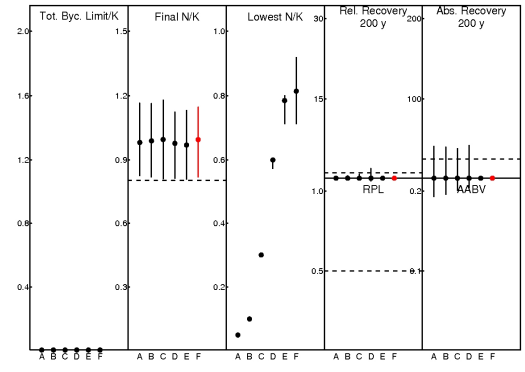
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (NoBycInitDep, EnvStoch20AC = 0, rmax = 2%)



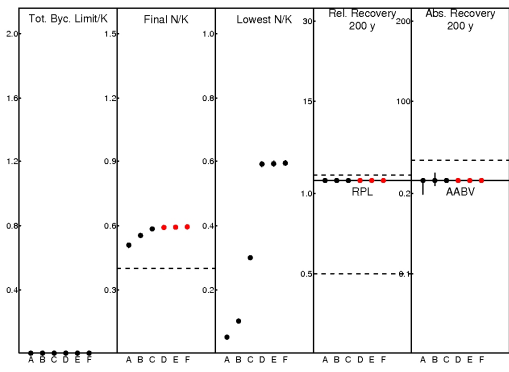
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (NoBycInitDep, EnvStoch20AC = 0, rmax = 4%)



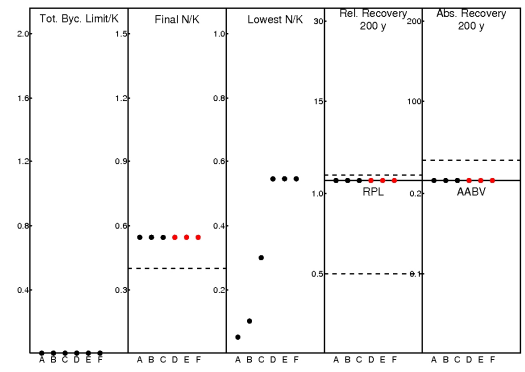
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (NoBycInItDep, EnvStoch20AC = 0.5, rmax = 2%)



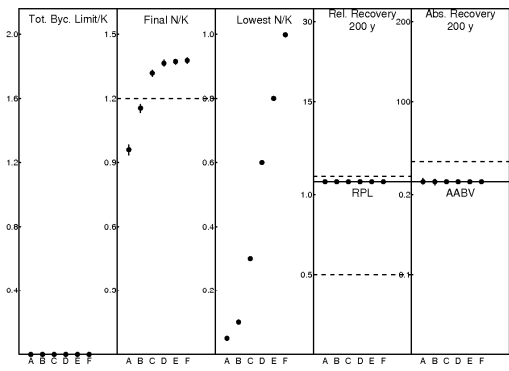
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (NoBycInItDep, EnvStoch20AC = 0.5, rmax = 4%)



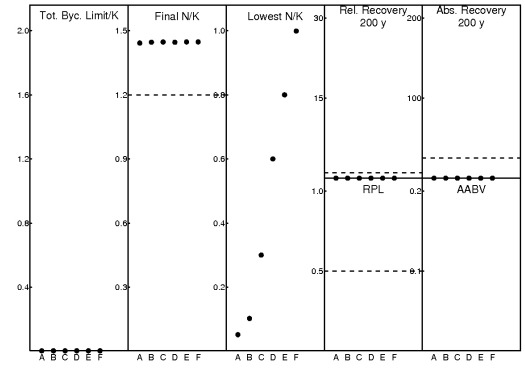
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (NoBycInItDep, KChange = 0.5, rmax = 2%)



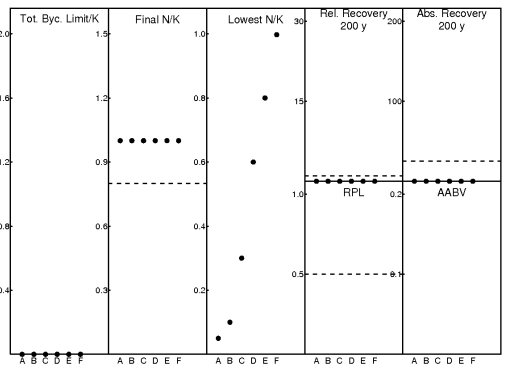
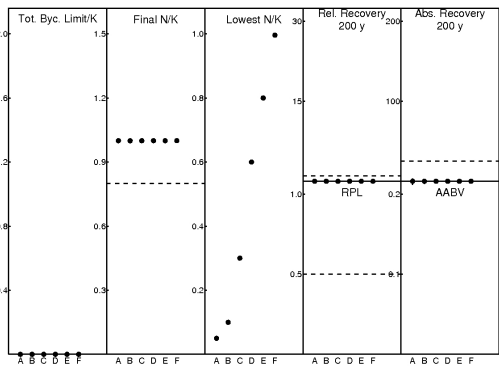
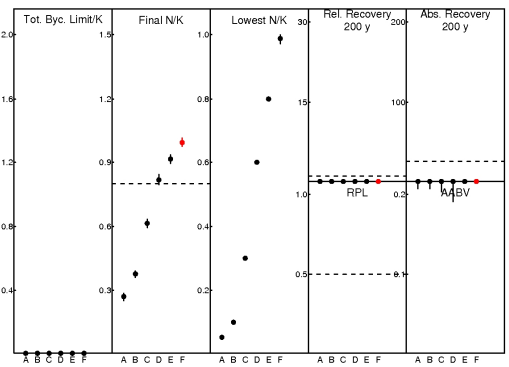
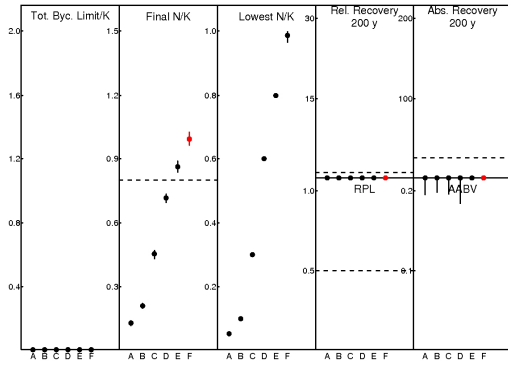
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (NoBycInItDep, KChange = 0.5, rmax = 4%)

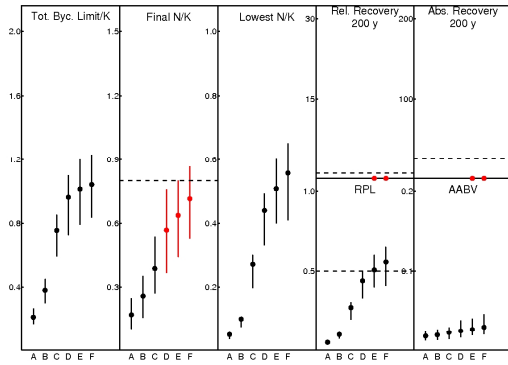


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (NoBycInItDep, KChange = 1.5, rmax = 2%)

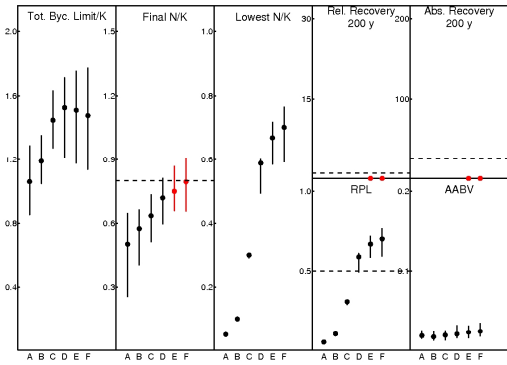


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (NoBycInItDep, KChange = 1.5, rmax = 4%)

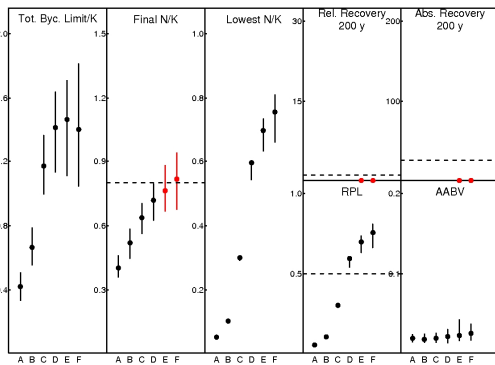




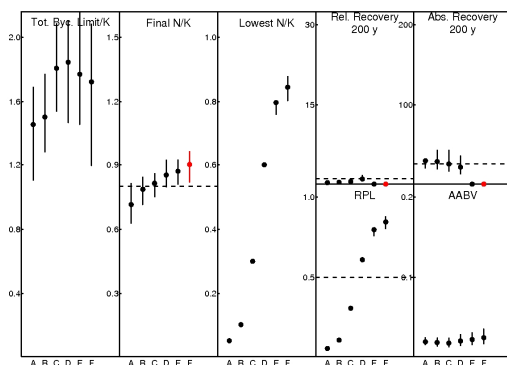
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CL11InitDep, Base = 1, rmax = 2%)



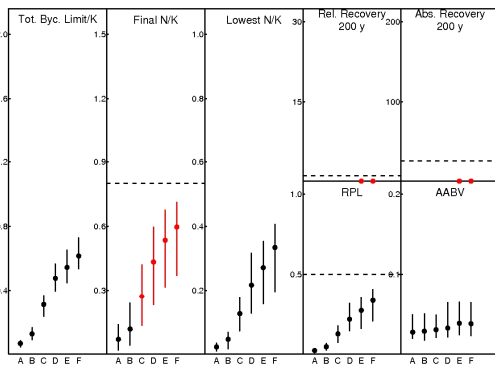
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CL11InitDep, Base = 1, rmax = 4%)



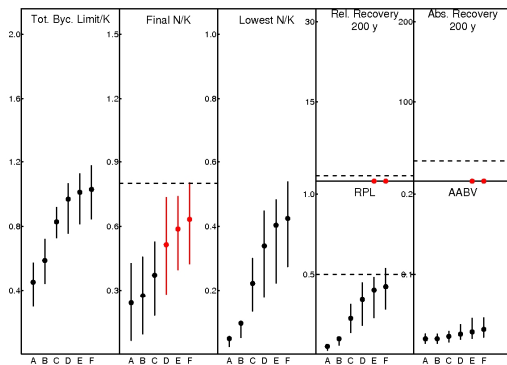
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CL11InitDep, BiasByc = 0.5, rmax = 2%)



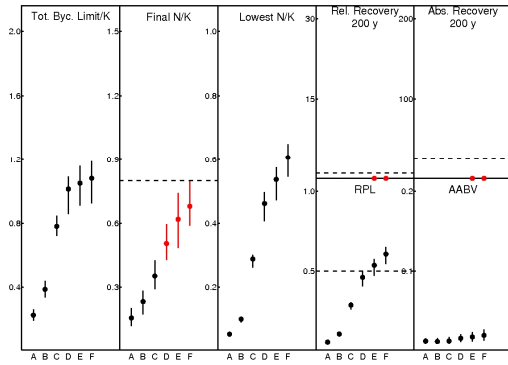
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CL11InitDep, BiasByc = 0.5, rmax = 4%)



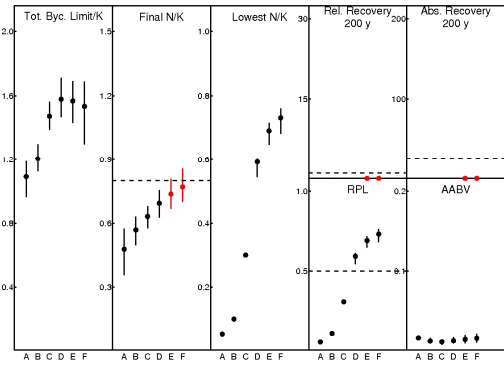
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CL11InitDep, BiasByc = 2, rmax = 2%)



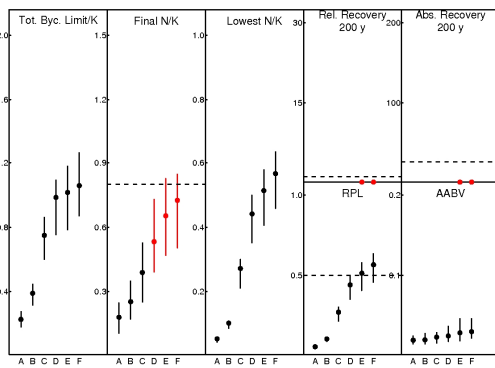
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CL11InitDep, BiasByc = 2, rmax = 4%)



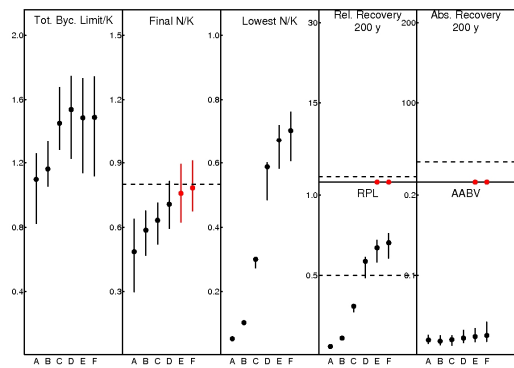
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, BiasSrvyCVAbs = 1, rmax = 2%)



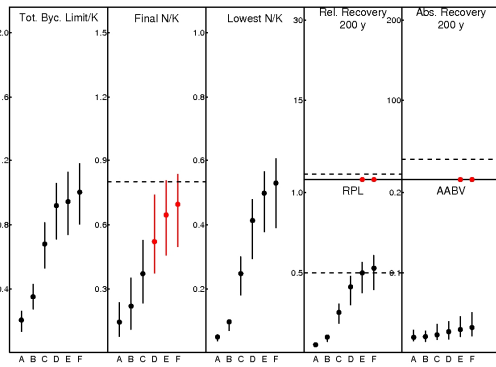
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, BiasSrvyCVAbs = 1, rmax = 4%)



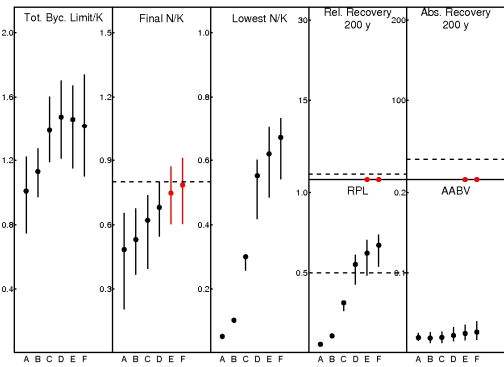
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, BycCV = 0.1, rmax = 2%)



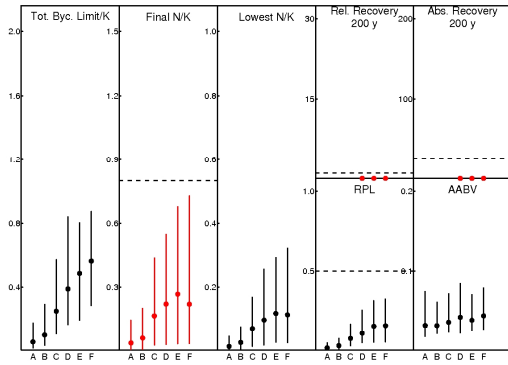
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, BycCV = 0.1, rmax = 4%)



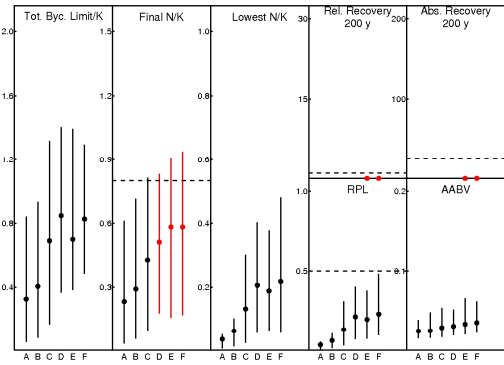
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, BycCV = 1, rmax = 2%)



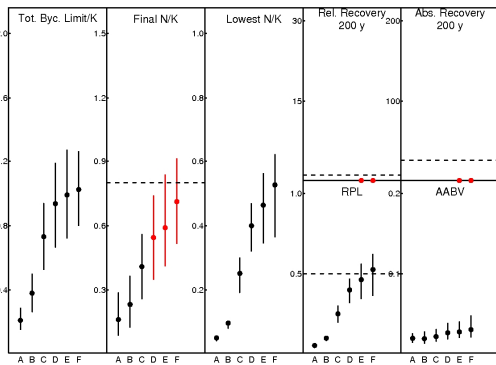
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, BycCV = 1, rmax = 4%)



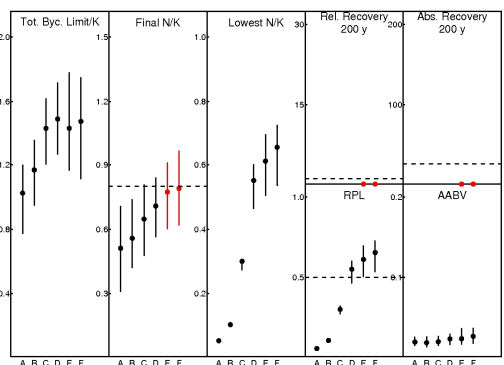
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, Cat = 1, rmax = 2%)



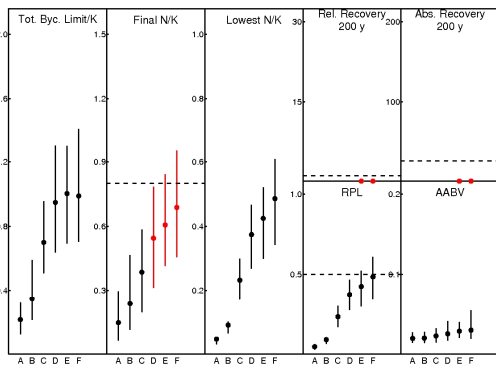
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, Cat = 1, rmax = 4%)



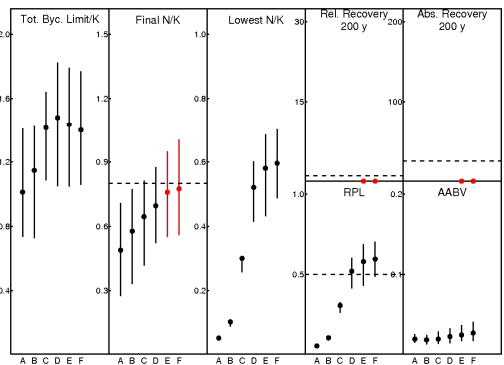
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, EnvStoch20AC = 0, rmax = 2%)



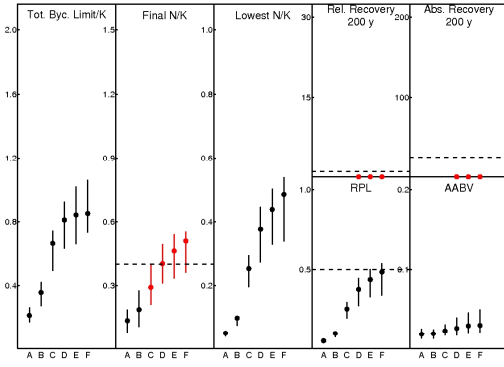
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, EnvStoch20AC = 0, rmax = 4%)



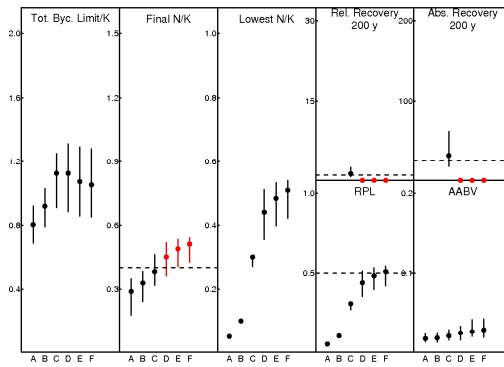
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, EnvStoch20AC = 0.5, rmax = 2%)



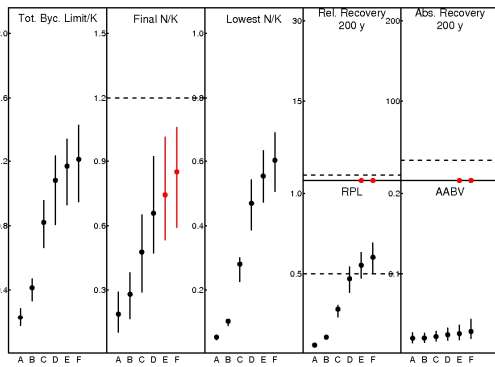
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, EnvStoch20AC = 0.5, rmax = 4%)



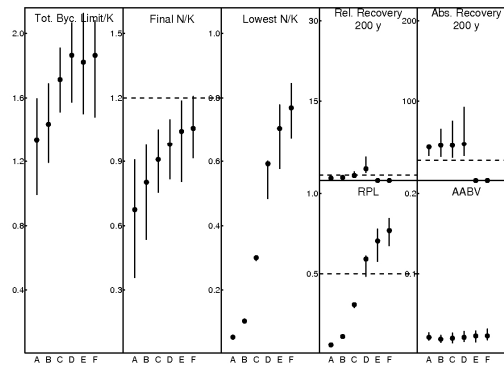
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, KChange = 0.5, rmax = 2%)



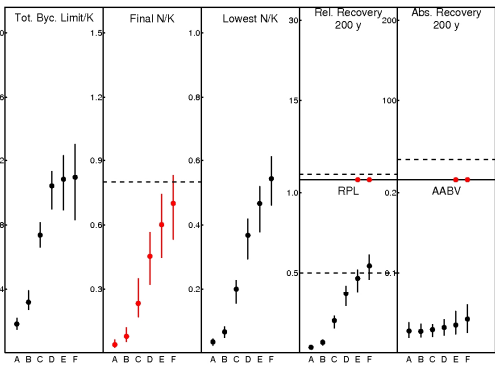
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, KChange = 0.5, rmax = 4%)



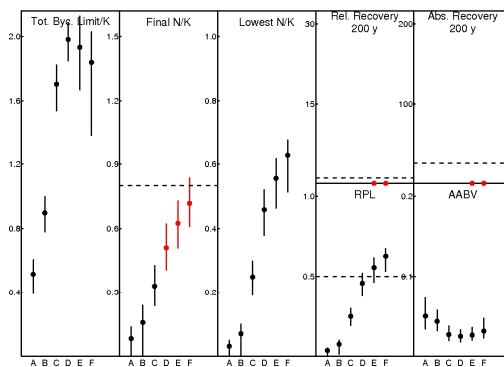
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, KChange = 1.5, rmax = 2%)



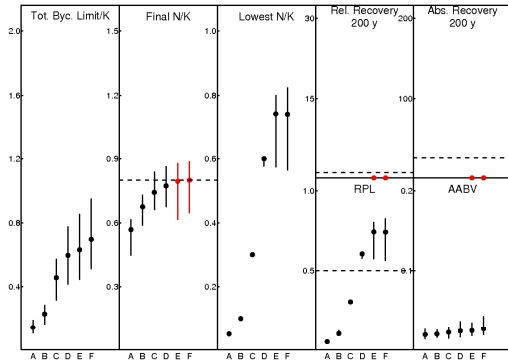
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, KChange = 1.5, rmax = 4%)



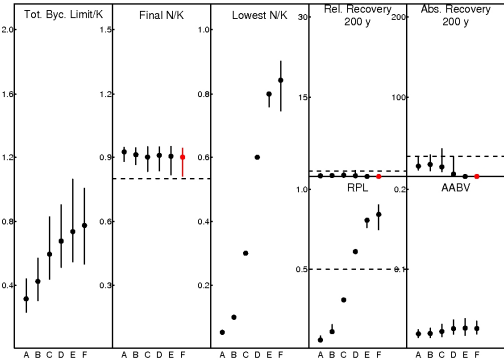
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, SrvyCVAbs = 0.1, rmax = 2%)



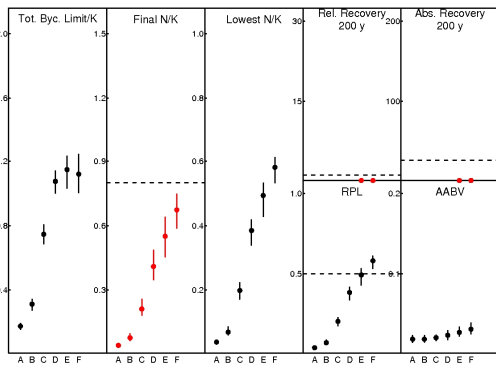
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, SrvyCVAbs = 0.1, rmax = 4%)



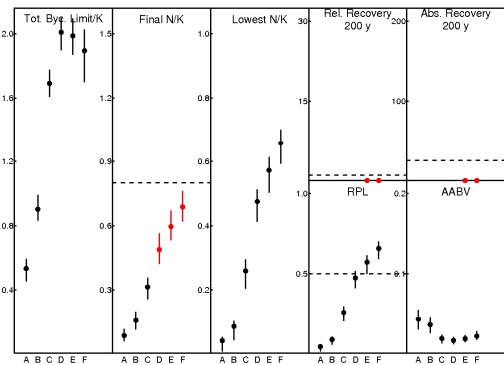
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, SrvyCVAbs = 0.6, rmax = 2%)



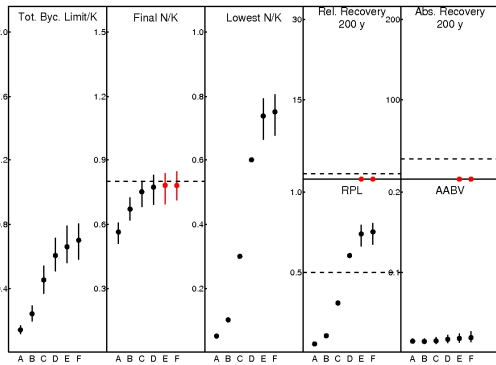
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, SrvyCVAbs = 0.6, rmax = 4%)



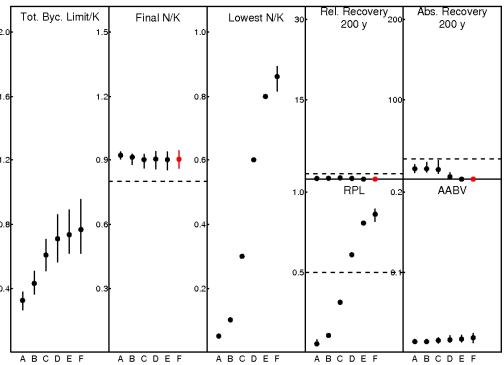
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, SrvyCVAbsUnbias = 0.1, rmax = 2%)



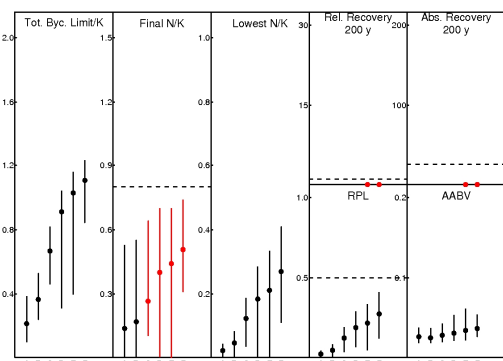
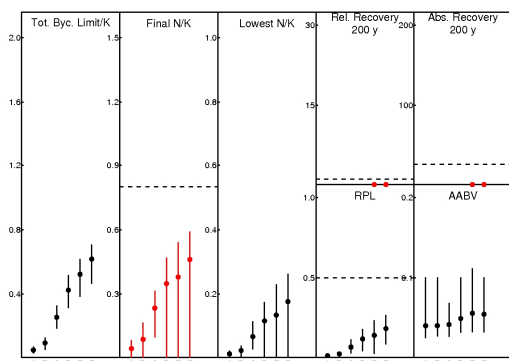
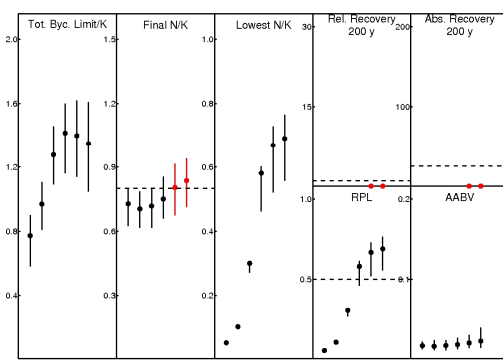
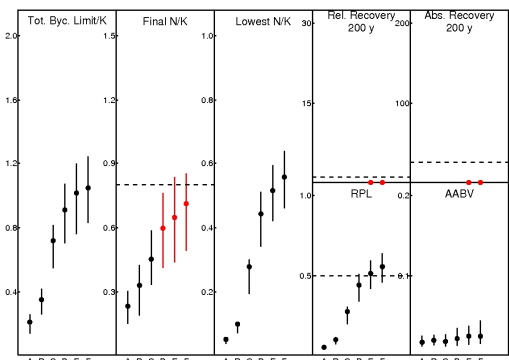
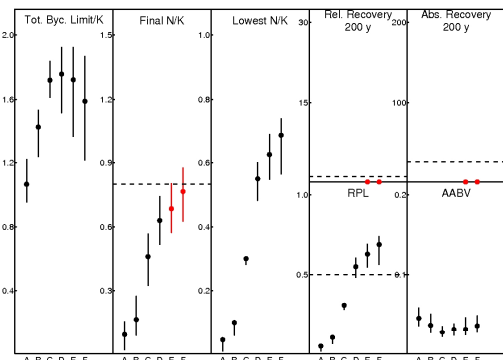
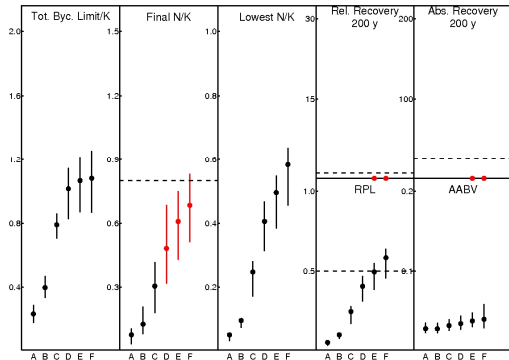
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, SrvyCVAbsUnbias = 0.1, rmax = 4%)

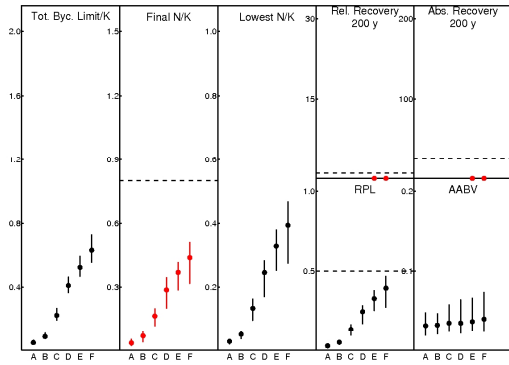


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, SrvyCVAbsUnbias = 0.6, rmax = 2%)

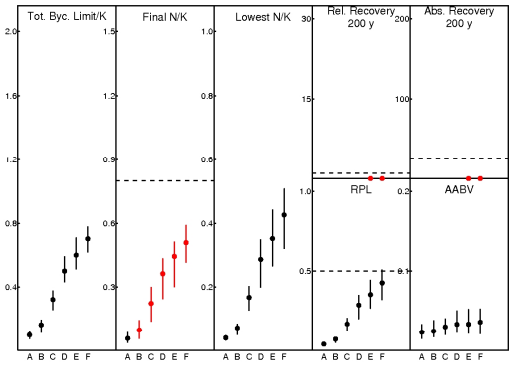


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, SrvyCVAbsUnbias = 0.6, rmax = 4%)

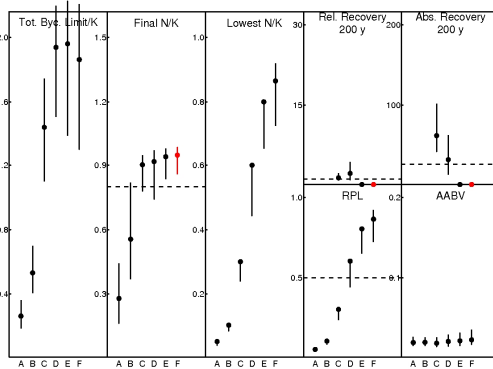




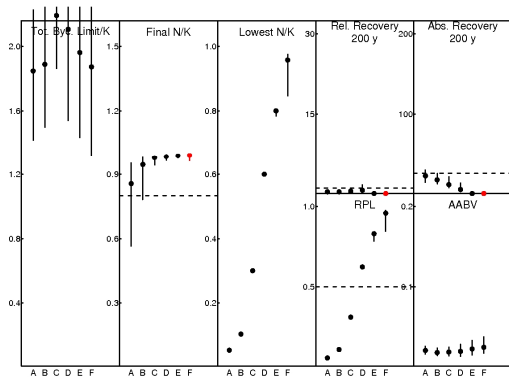
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, z = 0.1, rmax = 2%)



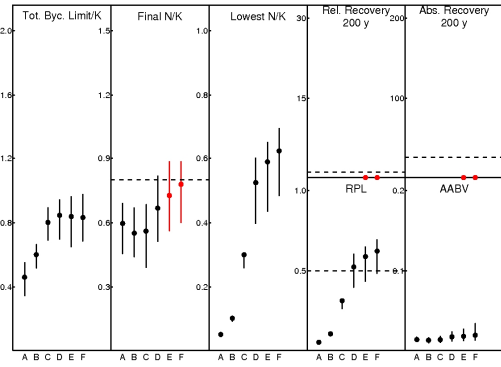
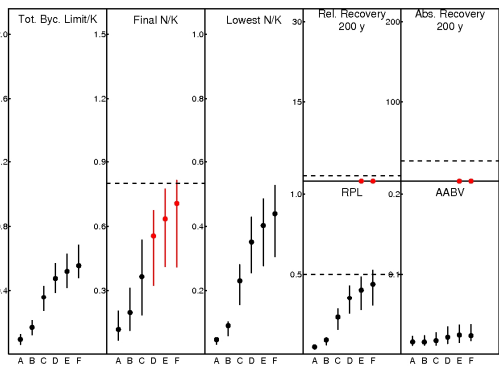
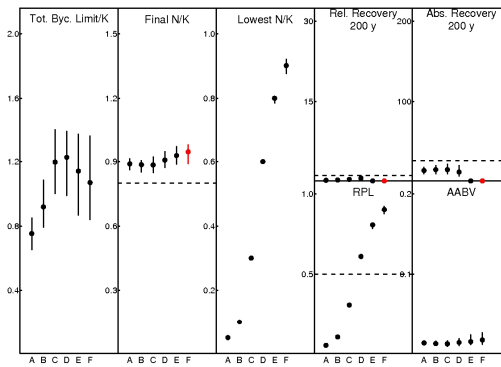
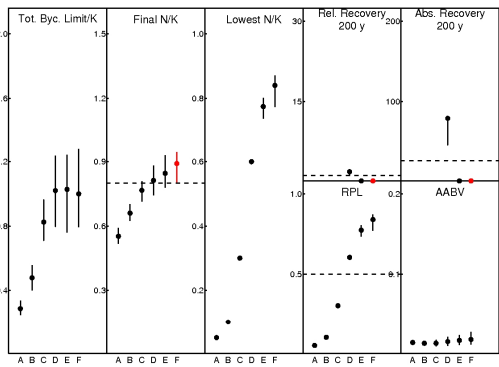
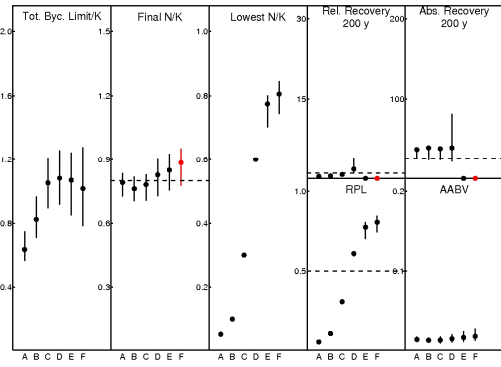
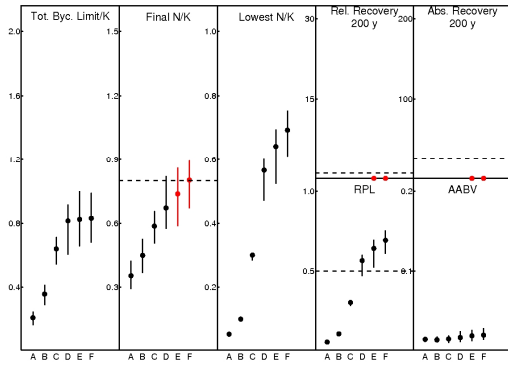
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, z = 0.1, rmax = 4%)

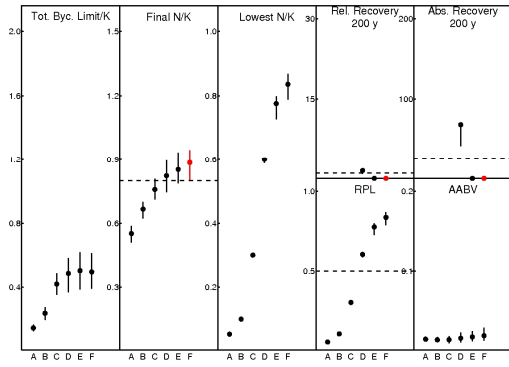


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, z = 13.5, rmax = 2%)

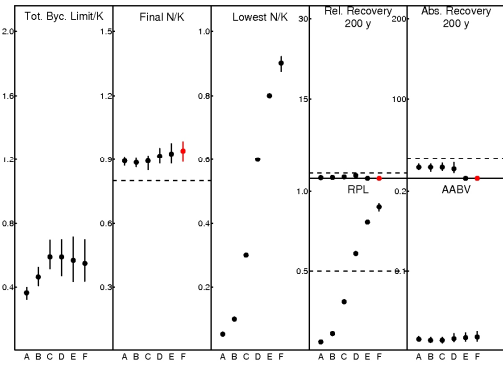


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA1InitDep, z = 13.5, rmax = 4%)

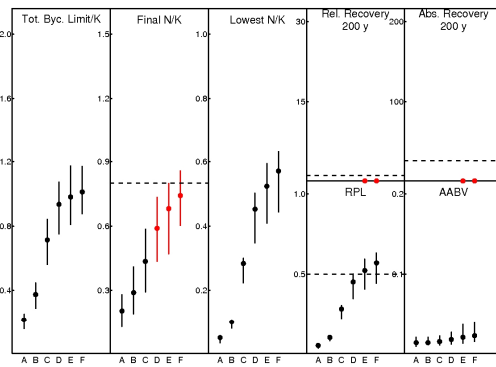




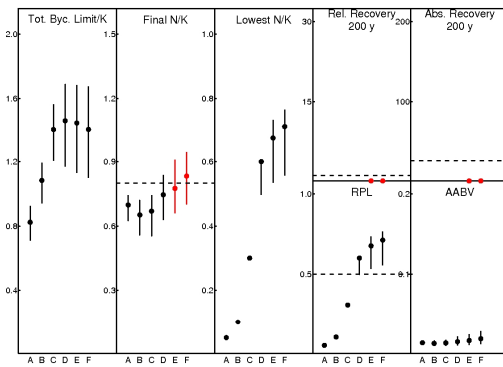
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, BiasSrvyAbs = 0.5, rmax = 2%)



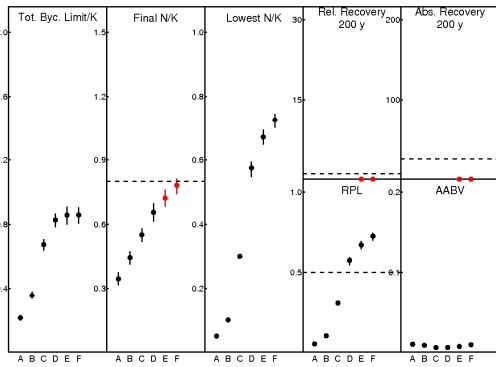
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, BiasSrvyAbs = 0.5, rmax = 4%)



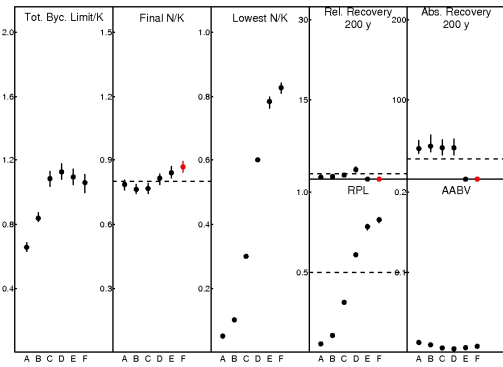
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, BiasSrvyAbs = 1.5, rmax = 2%)



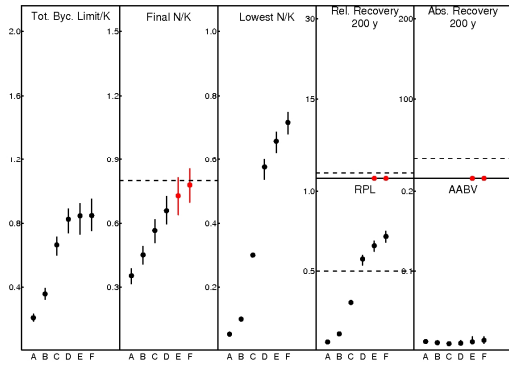
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, BiasSrvyAbs = 1.5, rmax = 4%)



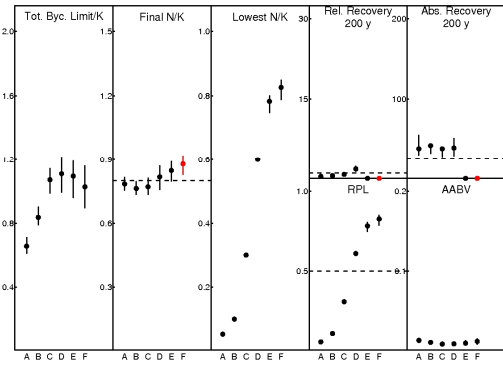
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, BiasSrvyCVAbs = 0.5, rmax = 2%)



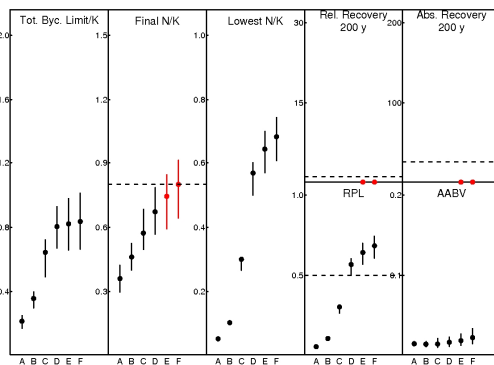
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, BiasSrvyCVAbs = 0.5, rmax = 4%)



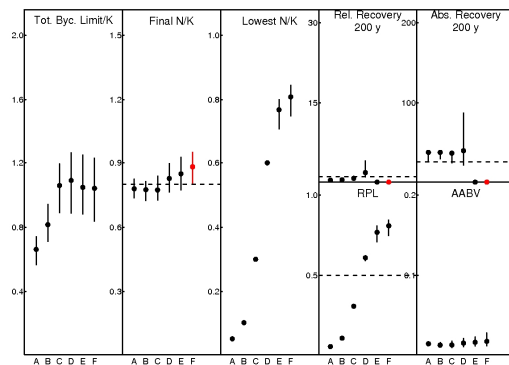
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, BiasSrvyCVAbs = 1, rmax = 2%)



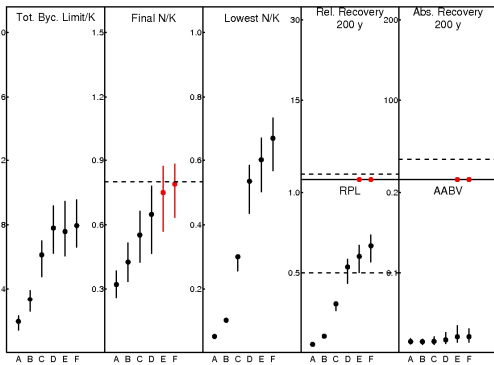
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, BiasSrvyCVAbs = 1, rmax = 4%)



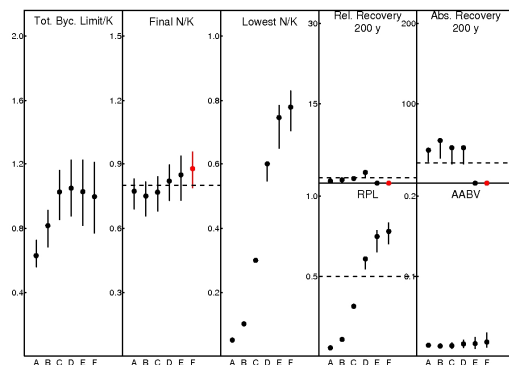
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, BycCV = 0.1, rmax = 2%)



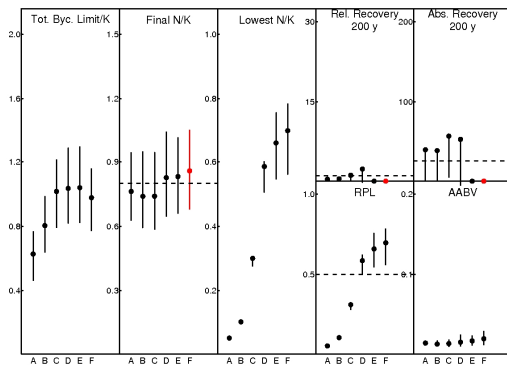
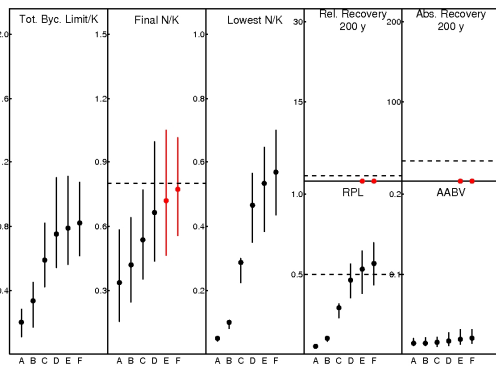
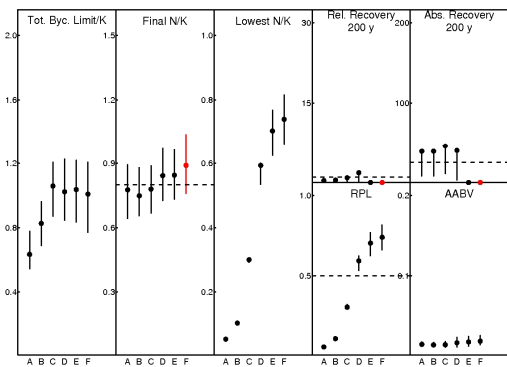
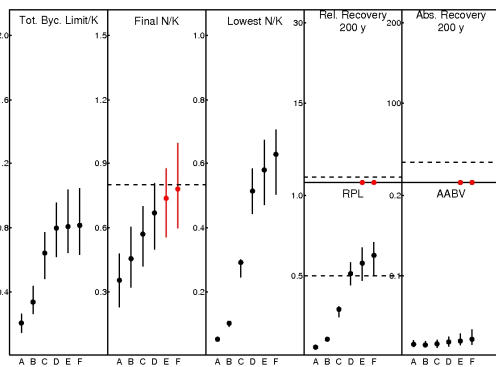
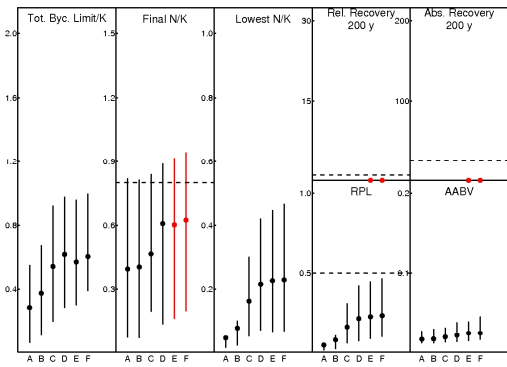
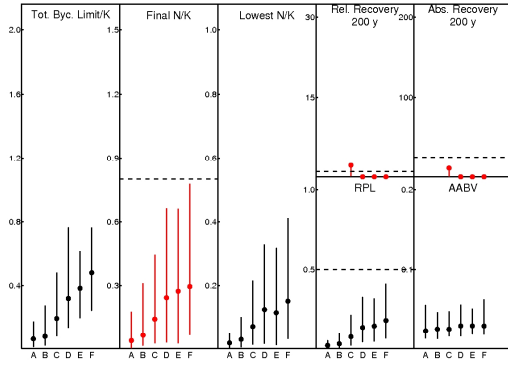
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, BycCV = 0.1, rmax = 4%)

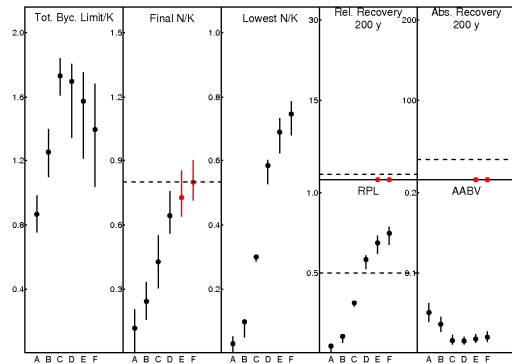
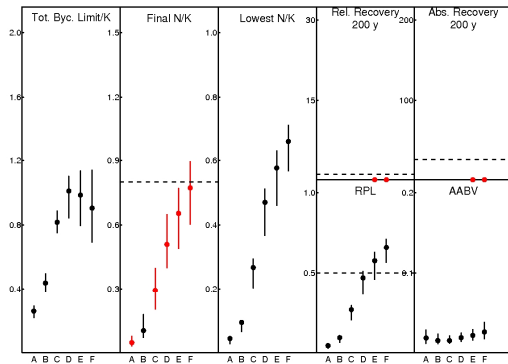
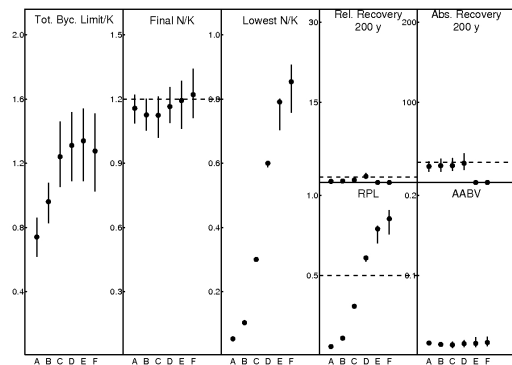
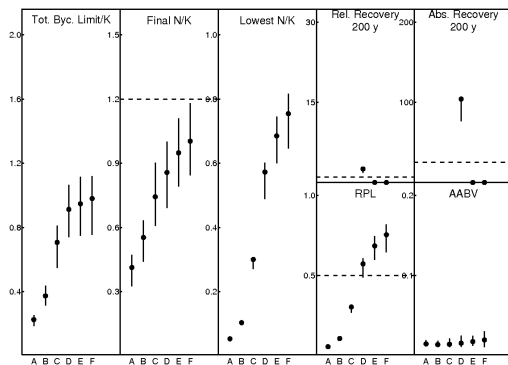
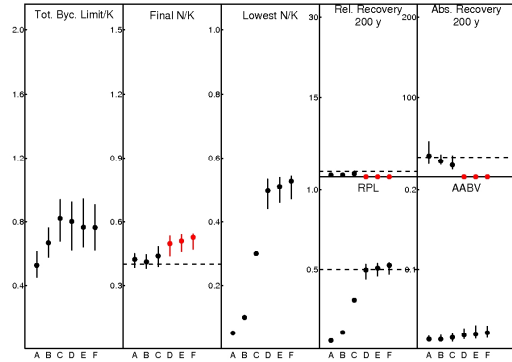
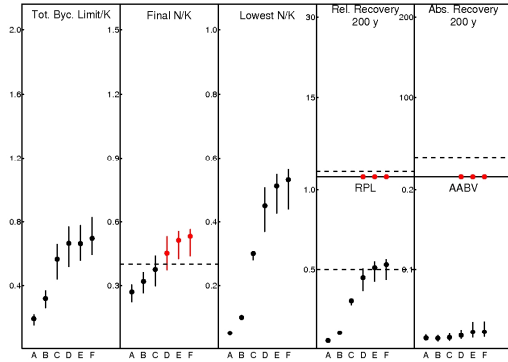


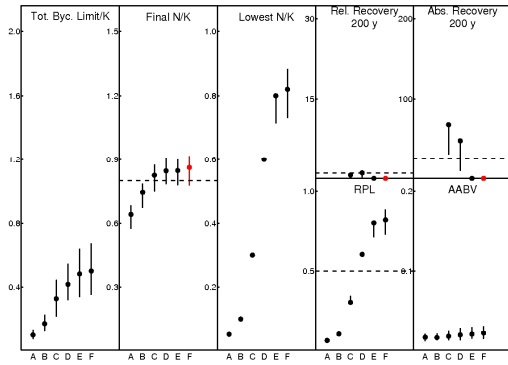
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, BycCV = 1, rmax = 2%)



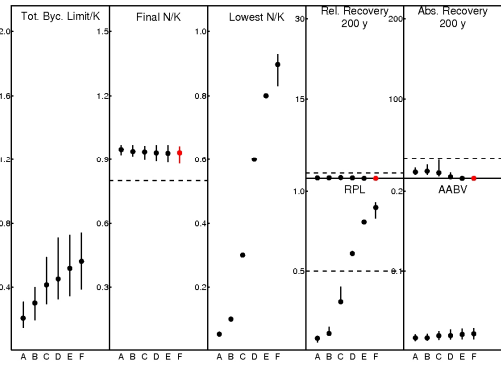
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, BycCV = 1, rmax = 4%)



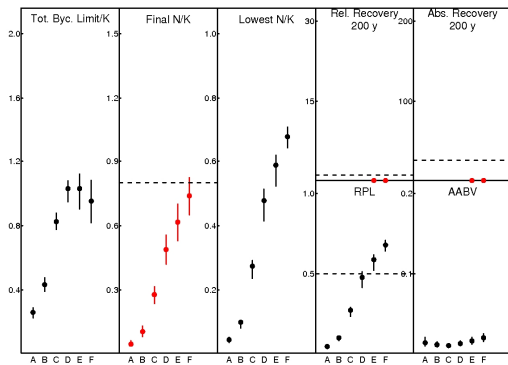




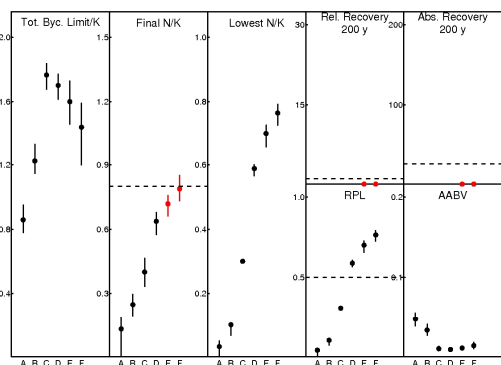
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, SrvyCVAbs = 0.6, rmax = 2%)



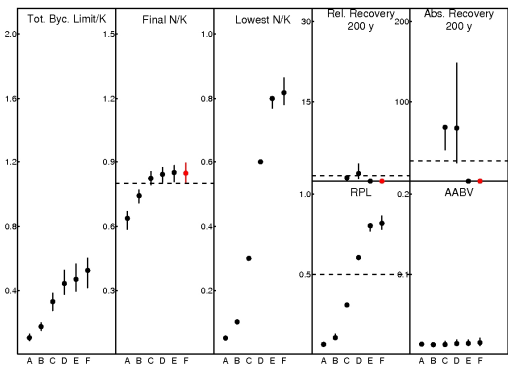
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, SrvyCVAbs = 0.6, rmax = 4%)



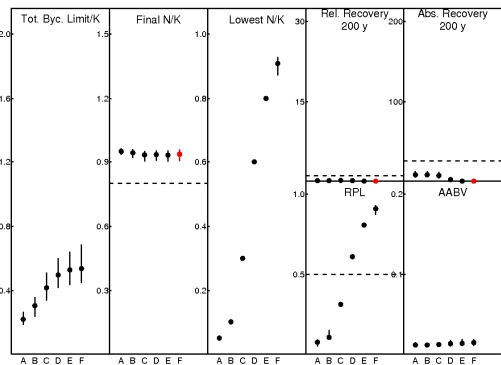
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, SrvyCVAbsUnbias = 0.1, rmax = 2%)



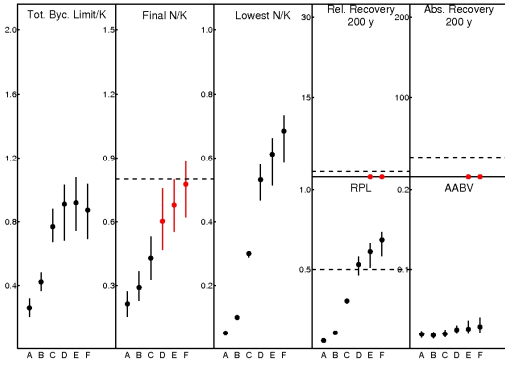
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, SrvyCVAbsUnbias = 0.1, rmax = 4%)



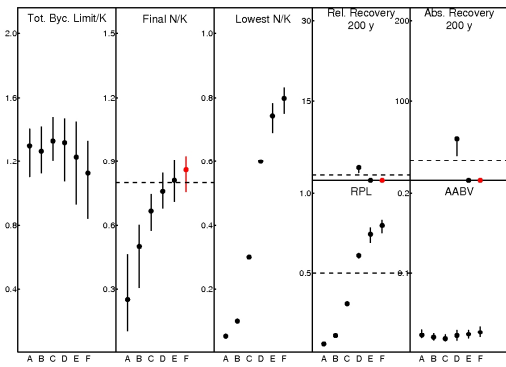
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, SrvyCVAbsUnbias = 0.6, rmax = 2%)



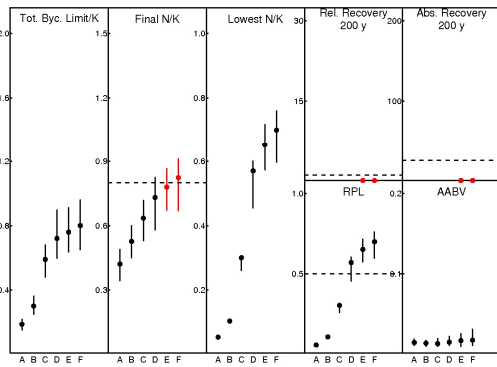
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, SrvyCVAbsUnbias = 0.6, rmax = 4%)



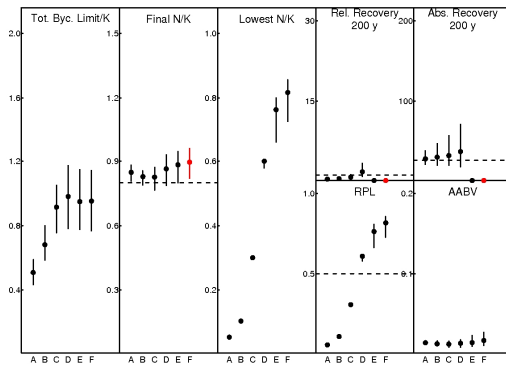
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, SrvyFreq = 5, rmax = 2%)



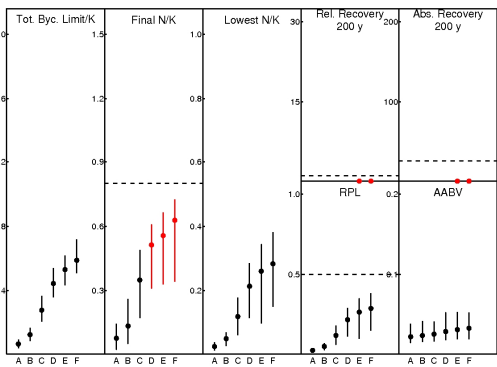
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, SrvyFreq = 5, rmax = 4%)



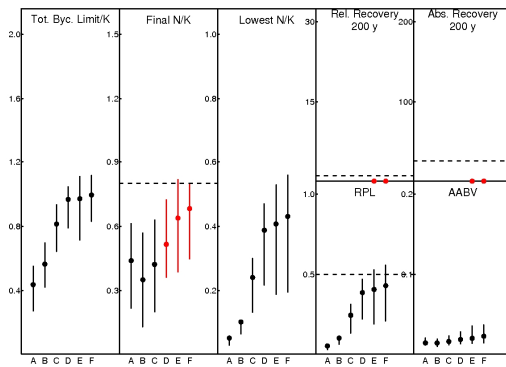
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, SrvyFreq = 15, rmax = 2%)



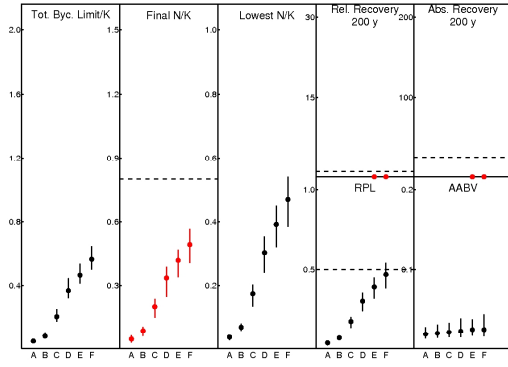
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, SrvyFreq = 15, rmax = 4%)



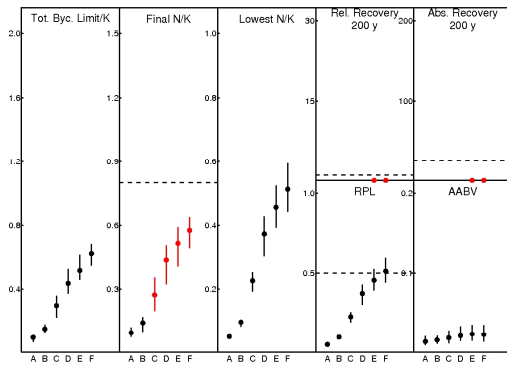
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, WorstCase = 1, rmax = 2%)



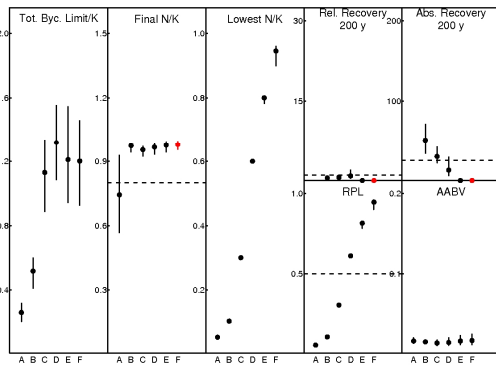
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, WorstCase = 1, rmax = 4%)



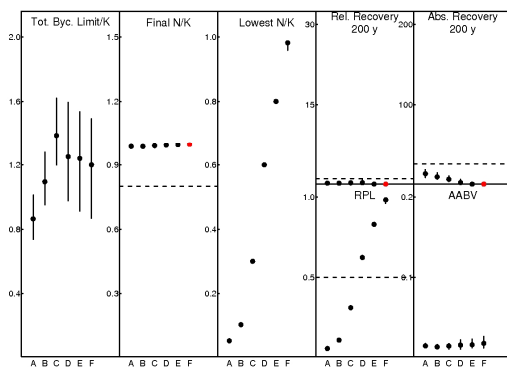
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, z = 0.1, rmax = 2%)



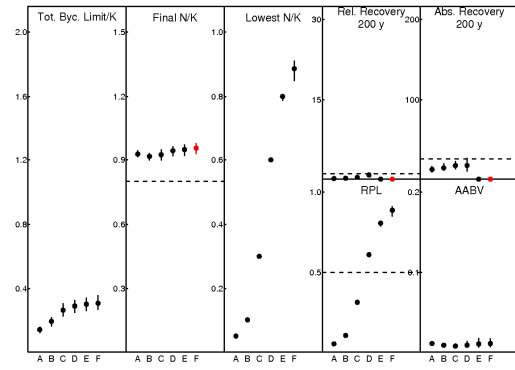
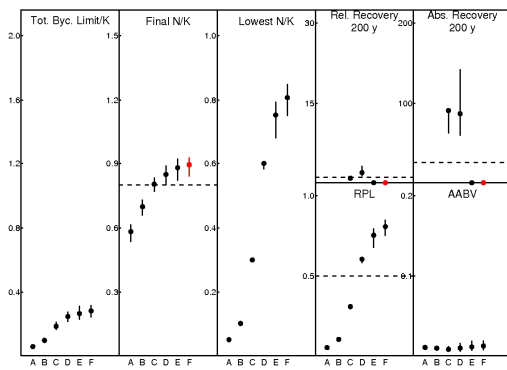
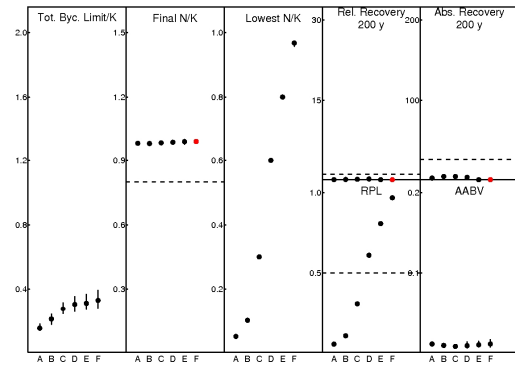
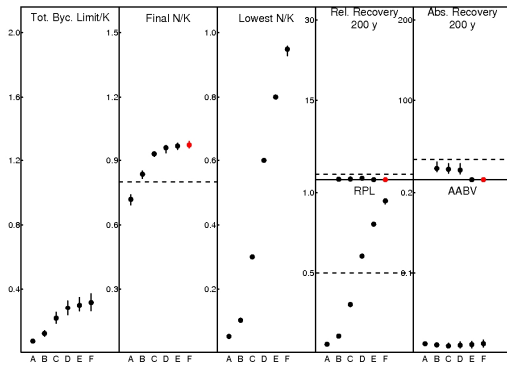
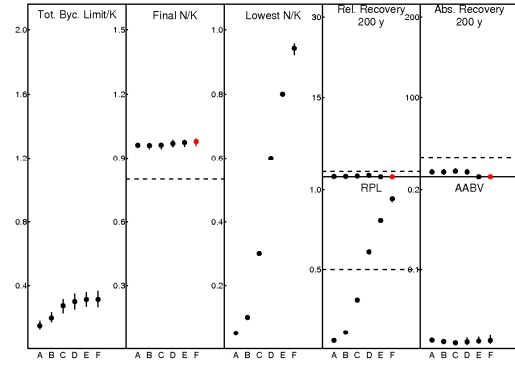
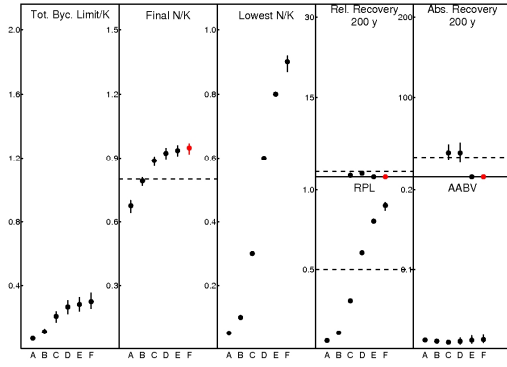
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, z = 0.1, rmax = 4%)

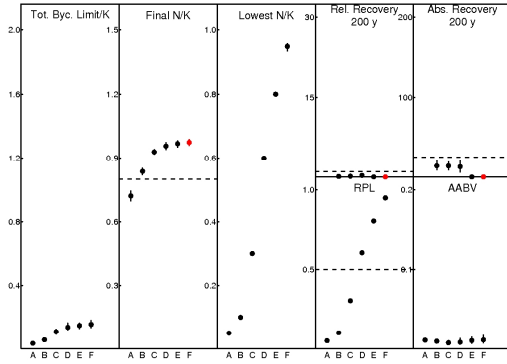


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, z = 13.5, rmax = 2%)

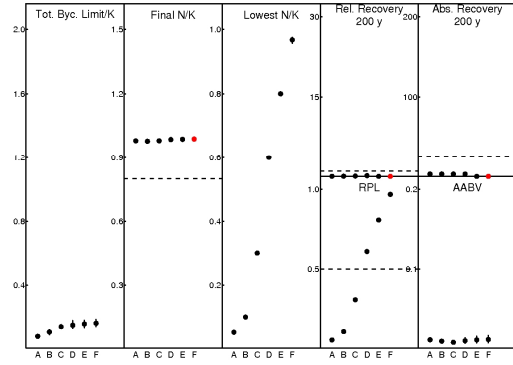


Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA2InitDep, z = 13.5, rmax = 4%)

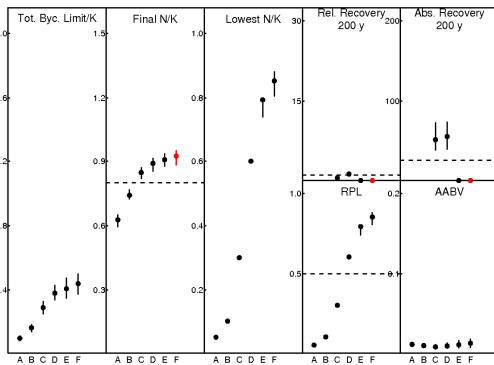




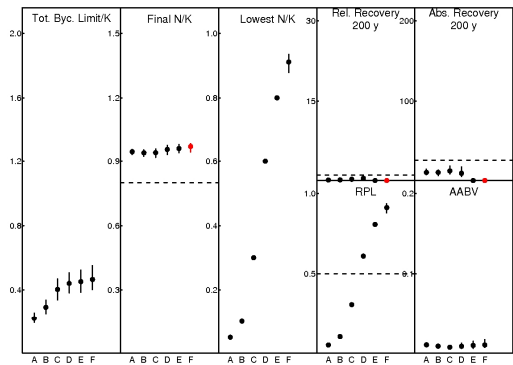
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CL3InitDep, BiasSrvyAbs = 0.5, rmax = 2%)



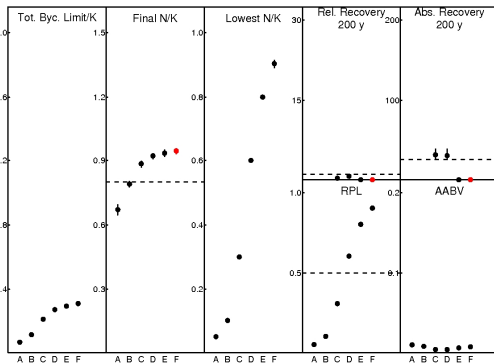
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CL3InitDep, BiasSrvyAbs = 0.5, rmax = 4%)



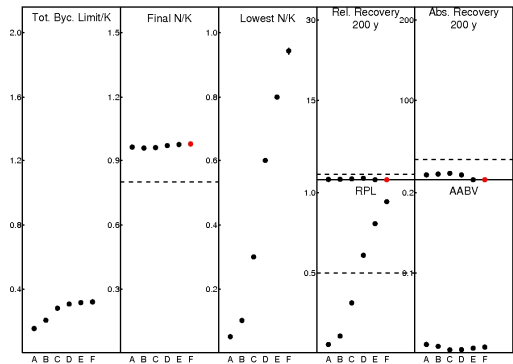
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CL3InitDep, BiasSrvyAbs = 1.5, rmax = 2%)



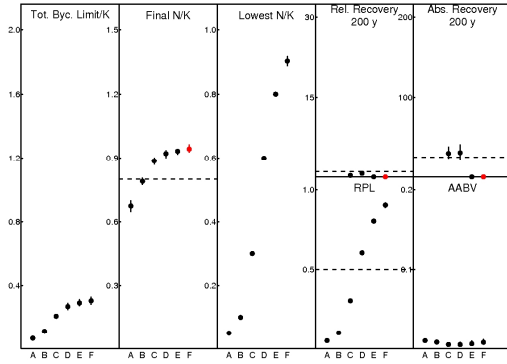
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CL3InitDep, BiasSrvyAbs = 1.5, rmax = 4%)



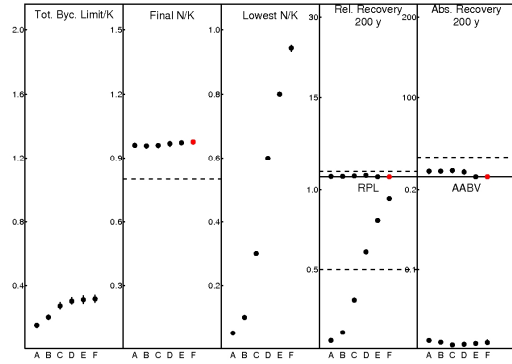
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CL3InitDep, BiasSrvyCVAbs = 0.5, rmax = 2%)



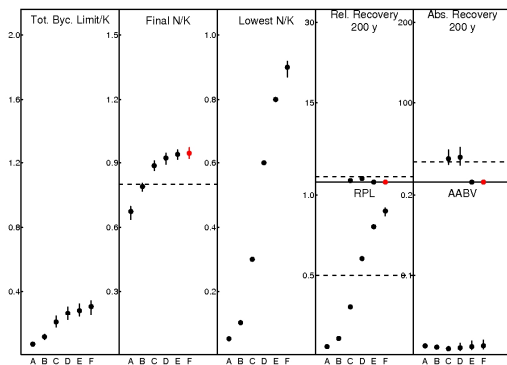
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CL3InitDep, BiasSrvyCVAbs = 0.5, rmax = 4%)



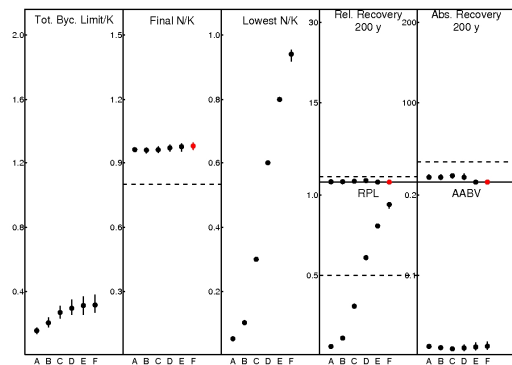
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, BiasSrvyCVAbs = 1, rmax = 2%)



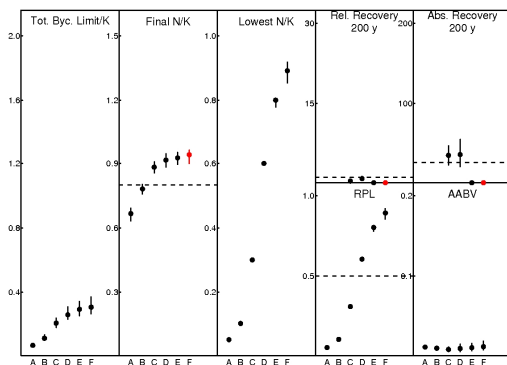
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, BiasSrvyCVAbs = 1, rmax = 4%)



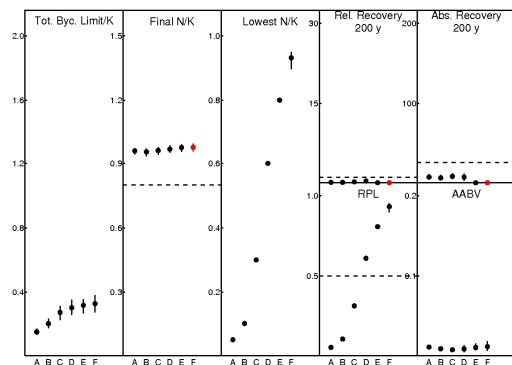
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, BycCV = 0.1, rmax = 2%)



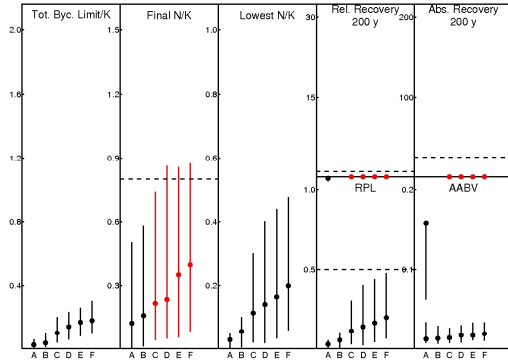
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, BycCV = 0.1, rmax = 4%)



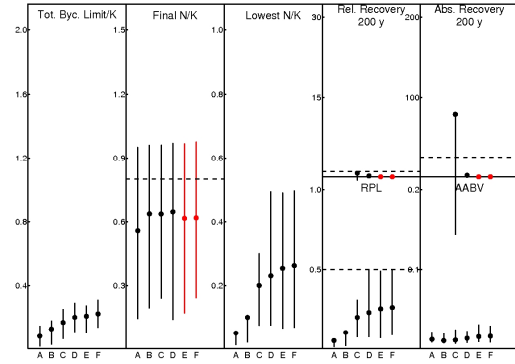
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, BycCV = 1, rmax = 2%)



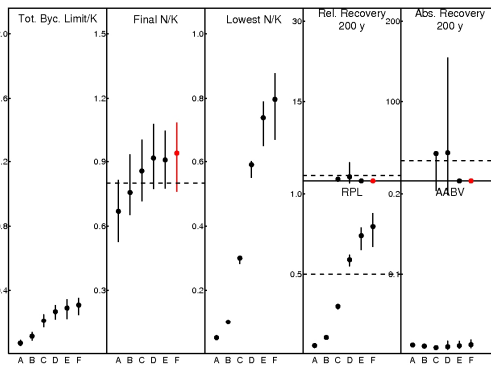
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, BycCV = 1, rmax = 4%)



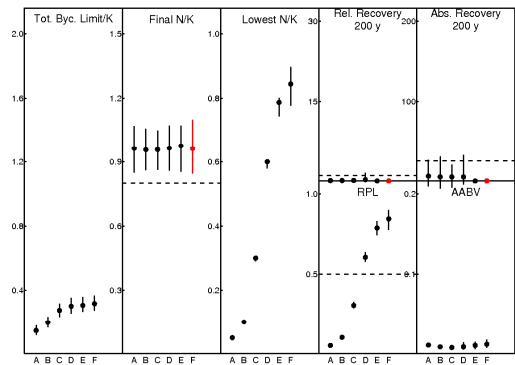
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, Cat = 1, rmax = 2%)



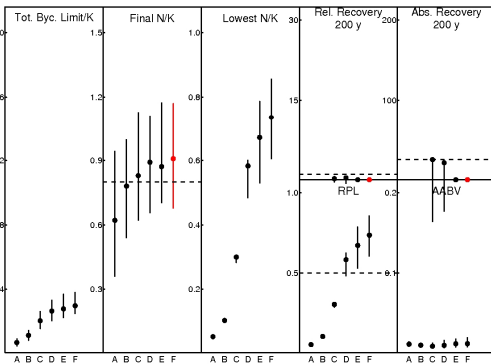
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, Cat = 1, rmax = 4%)



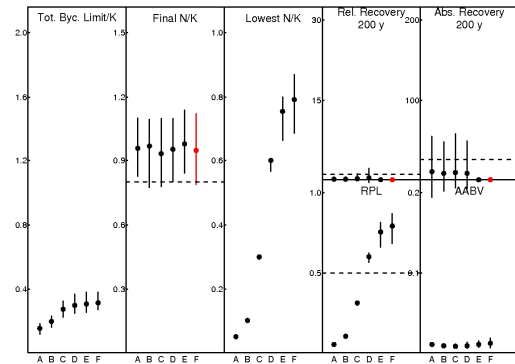
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, EnvStoch20AC = 0, rmax = 2%)



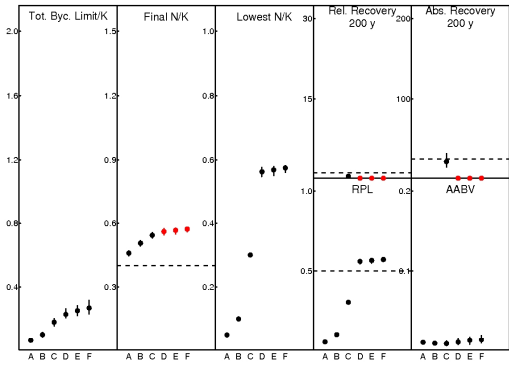
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, EnvStoch20AC = 0, rmax = 4%)



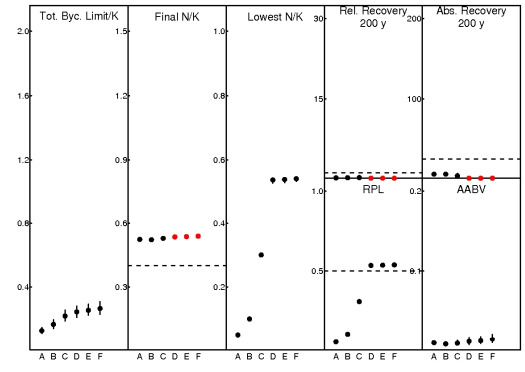
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, EnvStoch20AC = 0.5, rmax = 2%)



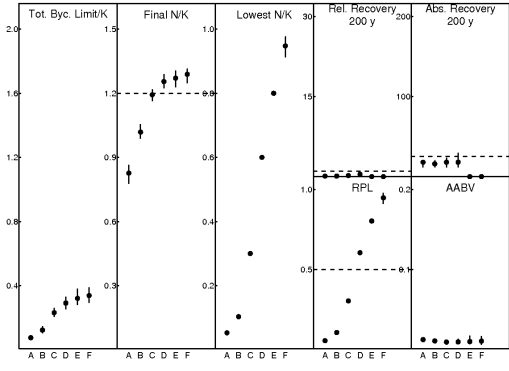
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, EnvStoch20AC = 0.5, rmax = 4%)



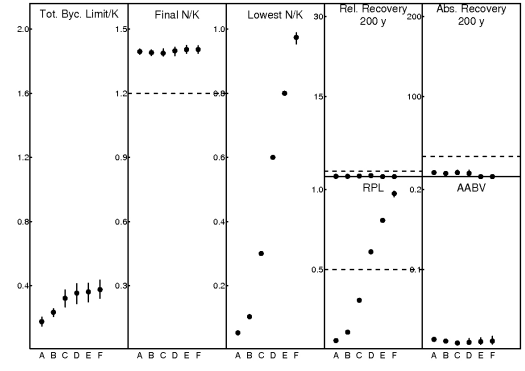
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, KChange = 0.5, rmax = 2%)



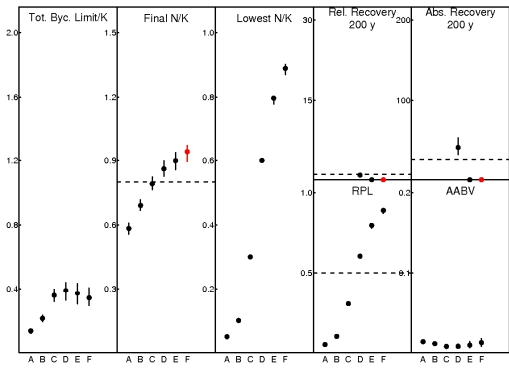
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, KChange = 0.5, rmax = 4%)



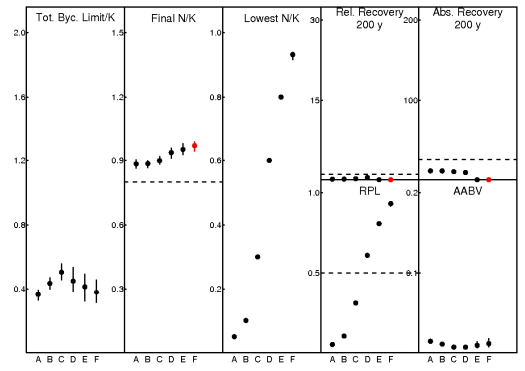
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, KChange = 1.5, rmax = 2%)



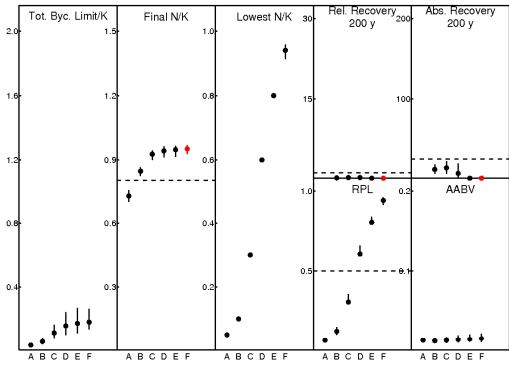
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, KChange = 1.5, rmax = 4%)



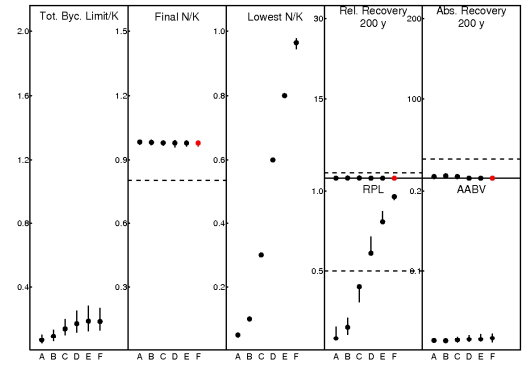
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, SrvyCVAbs = 0.1, rmax = 2%)



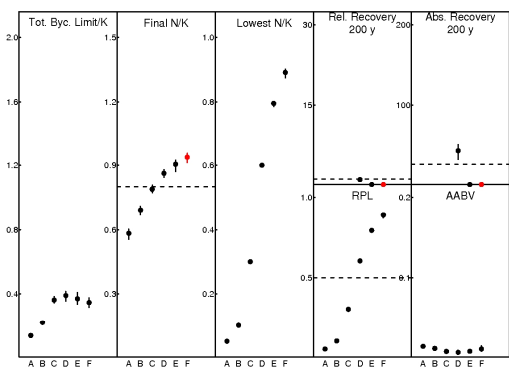
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, SrvyCVAbs = 0.1, rmax = 4%)



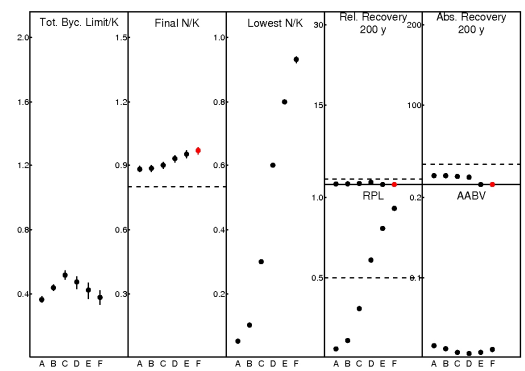
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, SrvyCVAbs = 0.6, rmax = 2%)



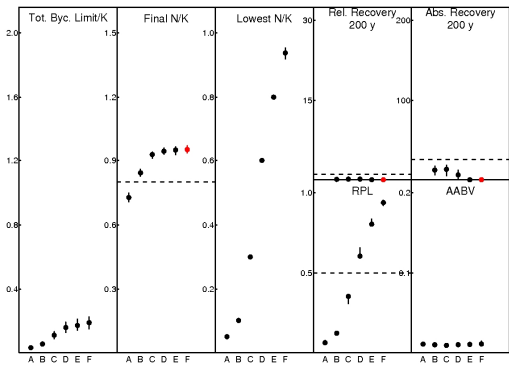
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, SrvyCVAbs = 0.6, rmax = 4%)



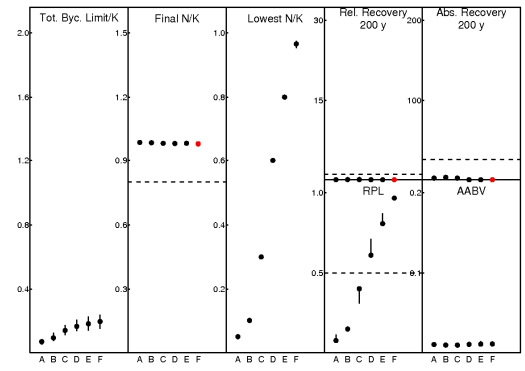
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, SrvyCVAbsUnbias = 0.1, rmax = 2%)



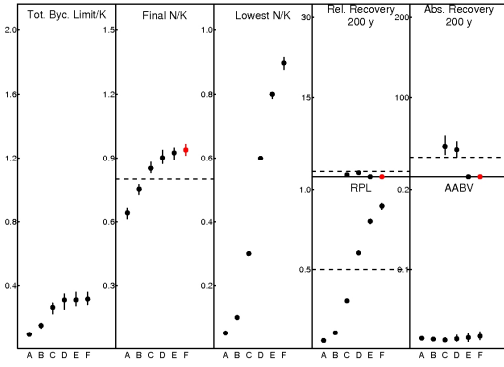
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, SrvyCVAbsUnbias = 0.1, rmax = 4%)



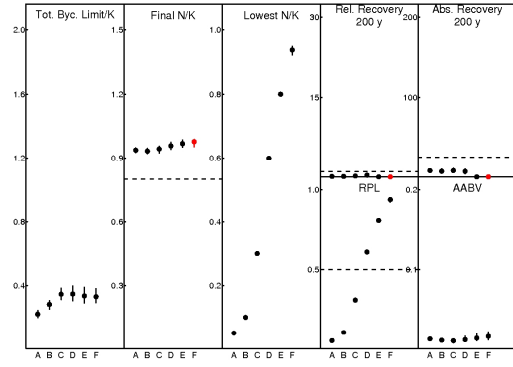
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, SrvyCVAbsUnbias = 0.6, rmax = 2%)



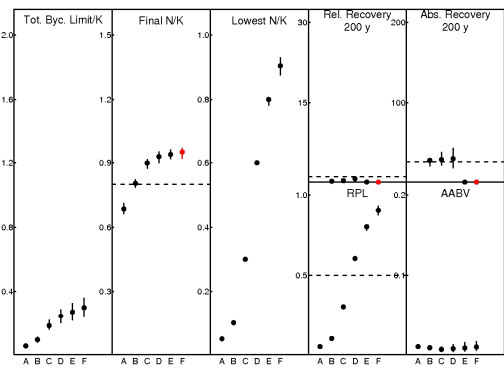
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, SrvyCVAbsUnbias = 0.6, rmax = 4%)



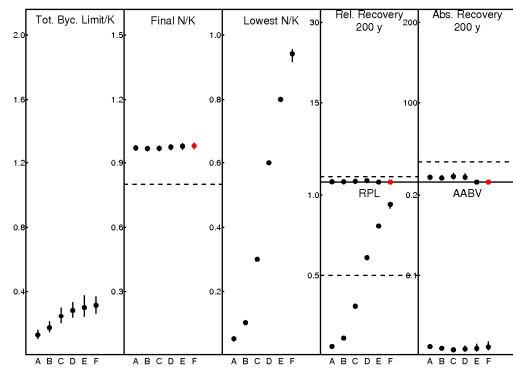
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, SrvyFreq = 5, rmax = 2%)



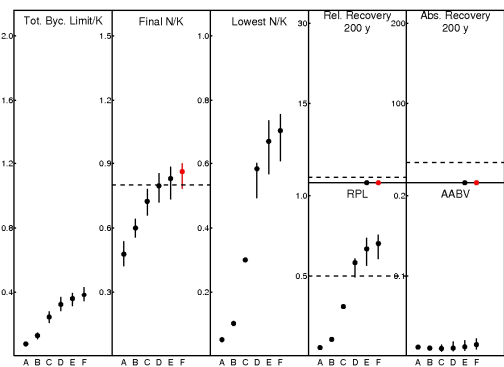
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, SrvyFreq = 5, rmax = 4%)



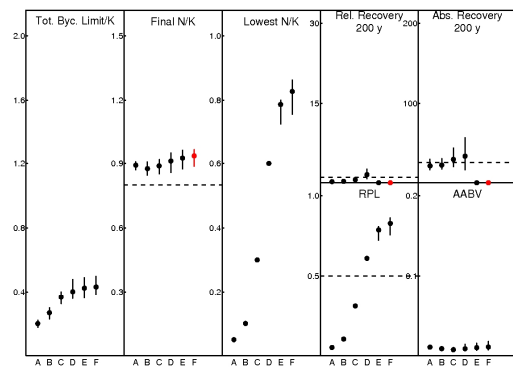
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, SrvyFreq = 15, rmax = 2%)



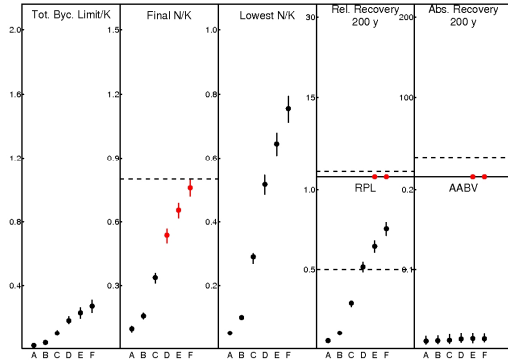
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, SrvyFreq = 15, rmax = 4%)



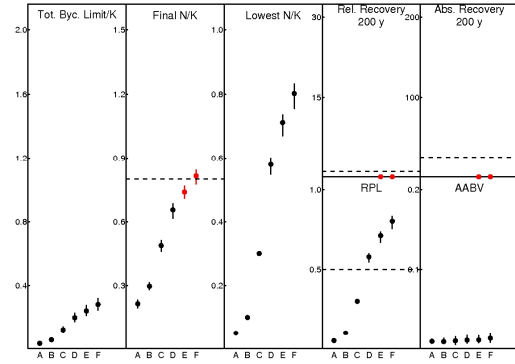
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, WorstCase = 1, rmax = 2%)



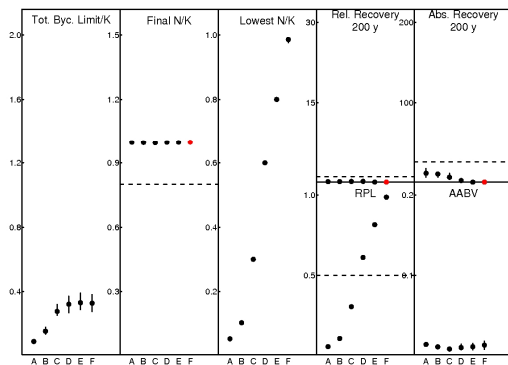
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, WorstCase = 1, rmax = 4%)



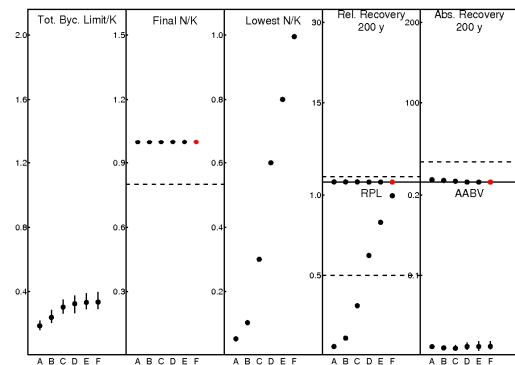
Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, z = 0.1, rmax = 2%)



Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, z = 0.1, rmax = 4%)



Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, z = 13.5, rmax = 2%)



Initial N/K: A=0.05 B=0.10 C=0.30 D=0.60 E=0.80 F=1
 (CLA3InitDep, z = 13.5, rmax = 4%)