



Population modelling of fish outcomes for the Reconnecting River Country Program: Carp

Final report for the NSW Department of Climate Change, Energy, the Environment and Water

Henry Wootton, Charles Todd,
John Koehn and Ivor Stuart

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Acknowledgment

We acknowledge and respect Victorian Traditional Owners as the original custodians of Victoria's land and waters, their unique ability to care for Country and deep spiritual connection to it. We honour Elders past and present whose knowledge and wisdom has ensured the continuation of culture and traditional practices.

We are committed to genuinely partner, and meaningfully engage, with Victoria's Traditional Owners and Aboriginal communities to support the protection of Country, the maintenance of spiritual and cultural practices and their broader aspirations in the 21st century and beyond.



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Final report for the NSW Department of Climate Change, Energy, the Environment and Water

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Contents

Acknowledgements	ii
Contents	iii
Tables	v
Figures	v
Summary	x
Context:	x
Methods:	x
Results:	xi
Conclusions:	xi
1 Introduction	1
1.1 Background to population models	2
2 Methods	11
2.1 Spatial area and population units	11
2.2 Program logic	11
2.3 Conceptual models	12
2.4 Ecological and operational workshops	12
2.5 Carp ecology	12
2.5.1 General biology	12
2.5.2 Reproductive biology	12
2.5.3 Recruitment	14
2.5.4 Growth	14
2.5.5 Survival	14
2.5.6 Ageing and longevity	15
2.5.7 Movements and dispersal	15
2.5.8 Habitats	15
2.5.9 Resistance and resilience	15
2.6 Carp population model description	15
2.6.1 Carp life cycle	16
2.6.2 Population dynamics	17
2.6.3 Aquatic habitats, river flows and floodplain inundation	21
2.7 Model construct	23
2.7.1 Model runs	23
2.8 Model inputs	24
2.8.1 Hydrology, gauges and inundation	24
2.9 Summary of model assumptions and limitations	26

2.10	Sensitivity analysis	26
2.11	Population responses for the period 1990–2019	27
2.12	Presentation of population model outputs	27
3	Results	28
3.1	Population modelling for scenarios	28
	Adult Carp mean population trajectories and expected mean population sizes	30
	Adult Carp mean population trajectories and expected mean population sizes for the hydrological years 1990–2019	39
	Early life-history responses of Carp	40
3.2	Interpreting hydrological inputs	41
3.3	Sensitivity analysis	41
4	Discussion	45
4.1	Key findings	45
4.2	Drivers of carp population responses under flow scenarios	47
4.3	Model sensitivity to Carp movement rates and population responses to differing habitats	48
4.4	Comparisons with native fish responses to considered flow scenarios	48
4.5	Future steps	49
4.6	Conclusions	49
5	References	51
6	Appendices	57
6.1	Appendix 1. Project team	57
6.2	Appendix 2. Description of habitat types used for Carp scenario modelling	58
6.3	Appendix 3. Survival rates for Carp in differing habitat types used in modelling	59
6.4	Appendix 4. Supplementary results	60
	Adult Carp expected minimum and maximum population sizes	61
	Adult Carp expected minimum and maximum population sizes for the years 1990–2019	70
	Early life-history responses of Carp	71
	Early life-history responses of Carp for the years 1990–2019	80
	Model sensitivity to assumptions about attractiveness of inundated floodplain habitats to Carp	81
	Sensitivity analysis of the different habitat types available as a means of exploring sensitivity to alternative configurations of early life-history survival	85
	Habitat inundation inputs for populations in this study	93

Tables

Table S1. Hydrological scenarios assessed for the Carp population modelling. Values represent the daily maximum flow rates for environmental flows at select gauge locations (i.e. flow limits).....x	
Table 1. Key concepts relating to the life stages of Carp outlined in Figure 16. 16	16
Table 2. Estimated Carp survival rates and associated standard deviation (S.D.) based upon hypothesised coefficient of variation (CV). 20	20
Table 3. RiM-FIM, EW-FIM, and CARM outputs have provided four habitat categories: ‘all other floodplain’ habitats; ‘permanent off-channel’ habitat; ‘permanent stream’ habitat, and ‘temporary waterbodies’ habitat. These habitat categories need to be aligned with those in the Carp model. We have aligned these habitats in Table 6. 22	22
Table 4. Description of habitat types used for Carp scenario modelling (from Koehn et al. 2016). 22	22
Table 5. Percentage Carp survival elicited from expert opinion and the associated growth rate for each habitat type (from Koehn et al. 2016). 22	22
Table 6. Habitats used for Carp modelling in each reach for flow scenarios. 23	23
Table 7. Flow scenarios assessed for the Carp population modelling. Values represent the daily maximum flow rates for environmental flows at select gauge locations (i.e. flow limits). 24	24
Table 8. Population units for Carp represented as for the modelling reported in this document (Figure 15). 26	26
Table 9: Sensitivity analysis of the matrix model in Figure 20, parameterised with survival rates from Table 2 and H3 from Table 5 as solutions to the characteristic polynomial ($CarpModel - \lambda I$) = 0 expressed as changes in the vital rates (parameter), the growth rate (λ) and percentage change in the growth rate from changes to the vital rates compared with H3: $\lambda = 1.0188$ 42	42
Table A2.1. Description of habitat types used for Carp scenario modelling (from Koehn et al. 2016). The present modelling utilised habitats #3, #6 #8, #9 and #10. 58	58
Table A3.1. Percentage survival elicited from expert opinion and the associated growth rate for each habitat type (from Koehn et al. 2016). 59	59

Figures

Figure S1. Modelled Carp adult population size across all modelled program reaches in the southern Murray–Darling Basin. Top panel: average adult population size; and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar. xii	xii
Figure 1. A conceptual example to demonstrate model outputs of population trajectories for four different management scenarios, with each coloured line representing a different management scenario (or a combination thereof). Three of the scenarios start with comparable population sizes, before one decreases (red), and the other two increase but at different rates (red and blue), whereas the size of the population stays relatively consistent through time in the fourth scenario (light brown). 3	3
Figure 2. A single trajectory from the total program populations of Carp for the Base case scenario. 4	4
Figure 3. Ten trajectories from the total program populations of Carp for the Base case scenario. The thicker yellow line represents the same trajectory as in Figure 2. 4	4
Figure 4. One hundred trajectories from the total program populations of Carp for the Base case scenario. The thicker yellow line represents the same trajectory as in Figure 2. 5	5
Figure 5. One thousand trajectories from the total program populations of Carp for the Base case scenario. The thicker yellow line represents the same trajectory as in Figure 2. 5	5
Figure 6. Summary of 1000 trajectories from the total population of Carp for the Base case scenario: the black line represents the mean population size through time; the blue lines represent ± 1 standard	

deviation from the mean; and the red dotted lines represent the maximum and minimum levels of the trajectories through time.	6
Figure 7. An example of the mean trajectories of three scenarios.	7
Figure 8. An example of the utility of comparing the distribution of minimum population sizes from the Figure 7 example. The green line reflects optimised management with lower numbers of Carp, the blue line reflects where the management of some threats have been addressed, and the red line reflects the poorest population outcome. These distributions represent the likelihood of the population falling below an identified threshold, with theoretical extinction occurring when this falls to zero. Key: min – minimum.	7
Figure 9. Bar chart of the expected minimum population size (+ 1 S.D.) from the Figure 7 example, where the percentage difference is always in reference to the expected minimum population size of the bar on the left (for model outputs this will be in comparison to the Base case scenario).	8
Figure 10. Indicative consequences when comparing the distribution of the mean population sizes from the Figure 7 example.	8
Figure 11. Bar chart of the expected mean population size (+ 1 S.D.) from the Figure 7 example, where the percentage difference is always in reference to the expected mean population size of the bar on the left.	9
Figure 12. Indicative consequences when comparing the cumulative distribution of maximum population sizes from the Figure 7 example.	9
Figure 13. Bar chart of the expected maximum population size (+ 1 S.D.) from the Figure 7 example, where the percentage difference is in reference to the expected minimum population size of the bar on the left.	10
Figure 14. Spatial structure of Carp populations modelled in the Murray–Darling Basin.	11
Figure 15. Schematic diagram of the various stages in the Carp life cycle. Note: young-of-the-year and subadults may both be referred to as ‘juveniles’.	16
Figure 16. (a) Life history stages of female Carp with time spent in each life stage and transition to the next stage; and (b) life stages converted to an annual time step with recruitment to one year old (1 y.o.) including the early life history stages and transition from one stage/age to the next expressed as a survival rate, where SE is egg survival; SL is larval survival; SF is fingerling survival; SY is young-of-the-year survival; S1 is one-year-old survival; S2 is two-year-old survival; and SA is generalised adult survival with 26 adult age classes used in the model.	18
Figure 17. Carp age frequency data with curve fitted to a fully represented section of the data.	19
Figure 18. Carp age-fecundity data with best fitting relationship shown with the blue line. Note that variation around the estimated relationship is generated (for use as a model input) to reflect variation in the empirical age-fecundity data (see Figure 19).	19
Figure 19. Generated Carp fecundity (‘000s) at age. The derived age-fecundity relationship (blue line and inset equation) as shown in Figure 18 is used to generate age-fecundity model inputs (black points). Empirical age-fecundity data are again shown with red points.	20
Figure 20. Age structured matrix model for Carp. Recruitment is in the top row and survival rates are in the subdiagonal, where recruitment to 1-year-olds is given by $R_{age} = Fecage \times Seggs \times Slarvae \times Sflings \times Syoy$. <i>Fecage</i> = the fecundity at a given age, <i>Seggs</i> = eggs survival, <i>Slarvae</i> = larvae survival, <i>Sflings</i> = fingerling survival and <i>Syoy</i> = young of year survival.	21
Figure 21. Modelled daily flow (in ML day-1) for the Wagga Wagga gauge on the Murrumbidgee River plotted through time in years for differing program scenarios.	25
Figure 22. Modelled Carp adult population size across all modelled program reaches in the southern Murray–Darling Basin. Top panel: predicted average adult population size, and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar.	30
Figure 23. Modelled Carp adult population size in all reaches in the Murray River (including the Edward River). Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar.	31

Figure 24. Modelled Carp adult population size in all reaches in the Murrumbidgee River. Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar.	32
Figure 25. Modelled Carp adult population size in the Hume to Yarrawonga reach (Murray River). Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar.	33
Figure 26. Modelled Carp adult population size in the Yarrawonga to Torrumbarry reach (Murray River). Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar.	34
Figure 27. Modelled Carp adult population size in the Torrumbarry to Wentworth reach (Murray River). Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar.	35
Figure 28. Modelled Carp adult population size in the Edward River. Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar.	36
Figure 29. Modelled Carp adult population size in the Gundagai to Hay reach (Murrumbidgee River). Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar.	37
Figure 30. Modelled Carp adult population size in the Hay to Balranald reach (Murrumbidgee River). Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar.	38
Figure 31. Modelled Carp adult population size across all modelled reaches in the southern Murray–Darling Basin for the hydrological years 1990–2019.	39
Figure 32. Predicted early life-history responses of Carp across all modelled program reaches in the southern Murray–Darling Basin.	40
Figure 33. Deviance plot of differing maximum yearly floodplain inundation under flow scenarios considered in this project.	41
Figure 34. Analytic sensitivity analysis of the matrix model in Figure 20 parameterised with survival rates from Table 2 and H3 from.	42
Figure 35. Hume to Yarrawonga expected values of the mean population size for the Base case (BC) and Option 4 (O4) for modelled Carp access to the floodplain, double rate of access to the floodplain (DR), and half rate of access to the floodplain (HR).	43
Figure 36. Yarrawonga to Torrumbarry expected values of the mean population size for the Base case (BC) and Option 4 (O4) for modelled Carp access to the floodplain, double rate of access to the floodplain (DR), and half rate of access to the floodplain (HR).	43
Figure 37. Edward River expected values of the mean population size for the Base case (BC) and Option 4 (O4) for modelled Carp access to the floodplain, double rate of access to the floodplain (DR), and half rate of access to the floodplain (HR).	44
Figure 38. Hay to Balranald expected values of the mean population size for the Base case (BC) and Option 4 (O4) for modelled Carp access to the floodplain, double rate of access to the floodplain (DR), and half rate of access to the floodplain (HR).	44
Figure 39. Total Carp Base Case trajectories, total Carp count data (red line) and best fit trajectory (blue line) in the left panel and total Carp Option 4 trajectories, total Carp count data (red line) and best fit trajectory (blue line) in the right panel.	45
Figure A4.1. Modelled Carp adult population responses across all modelled reaches in the southern Murray–Darling Basin.	61
Figure A4.2. Modelled Carp adult population responses across all populations in the Murray River.	62
Figure A4.3. Modelled Carp adult population responses across all populations in the Murrumbidgee River.	63
Figure A4.4. Modelled Carp adult population in the Hume to Yarrawonga reach (Murray River).	64
Figure A4.5. Modelled Carp adult population in the Yarrawonga to Torrumbarry reach (Murray River).	65
Figure A4.6. Modelled Carp adult population in the Torrumbarry to Wentworth reach (Murray River).	66

Figure A4.7. Modelled Carp adult population in the Edward River.	67
Figure A4.8. Modelled Carp adult population in the Gundagai to Hay reach (Murrumbidgee River).	68
Figure A4.9. Modelled Carp adult population in the Hay to Balranald reach (Murrumbidgee River).	69
Figure A4.10. Modelled Carp adult population responses across all modelled reaches in the southern Murray–Darling Basin for the years 1990–2019.	70
Figure A4.11. Predicted early life-history responses of Carp across all modelled program reaches in the southern Murray–Darling Basin.	71
Figure A4.12. Predicted early life-history responses of Carp across all modelled reaches in the Murray River (including the Edward River).	72
Figure A4.13. Predicted early life-history responses of Carp across both modelled reaches in the Murrumbidgee River.	73
Figure A4.14. Predicted early life-history responses of Carp in the Hume to Yarrawonga reach (Murray River).	74
Figure A4.15. Predicted early life-history responses of Carp in the Yarrawonga to Torrumbarry reach (Murray River).	75
Figure A4.16. Predicted early life-history responses of Carp in the Torrumbarry to Wentworth reach (Murray River).	76
Figure A4.17. Predicted early life-history responses of Carp in the Edward River.	77
Figure A4.18. Predicted early life-history responses of Carp in the Gundagai to Hay reach (Murrumbidgee River).	78
Figure A4.19. Predicted early life-history responses of Carp in the Hay to Balranald reach (Murrumbidgee River).	79
Figure A4.20. Predicted early life-history responses of Carp across all modelled program reaches in the southern Murray–Darling Basin for the years 1990–2019.	80
Figure A4.21. Hume to Yarrawonga expected values of the mean population size for the Base case (BC) and Option 4 (O4) for modelled Carp access to the floodplain, double rate of access to the floodplain (DR), and half rate of access to the floodplain (HR).	81
Figure A4.22. Yarrawonga to Torrumbarry expected values of the mean population size for the Base case (BC) and Option 4 (O4) for modelled Carp access to the floodplain, double rate of access to the floodplain (DR), and half rate of access to the floodplain (HR).	82
Figure A4.23. Edward River expected values of the mean population size for the Base case (BC) and Option 4 (O4) for modelled Carp access to the floodplain, double rate of access to the floodplain (DR), and half rate of access to the floodplain (HR).	83
Figure A4.24. Hay to Balranald expected values of the mean population size for the Base case (BC) and Option 4 (O4) for modelled Carp access to the floodplain, double rate of access to the floodplain (DR), and half rate of access to the floodplain (HR).	84
Figure A4.25. Habitat 1 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 0.77.	85
Figure A4.26. Habitat 2 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 0.88.	86
Figure A4.27. Habitat 3 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 1.02.	86
Figure A4.28. Habitat 4 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 0.86.	87
Figure A4.29. Habitat 5 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 1.06.	87
Figure A4.30. Habitat 6 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 2.43.	88
Figure A4.31. Habitat 7 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 1.52.	88

Figure A4.32. Habitat 8 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 1.46.....	89
Figure A4.33. Habitat 9 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 1.78.....	89
Figure A4.34. Habitat 10 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 2.41.....	90
Figure A4.35. Habitat 11 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 2.6.....	90
Figure A4.36. Habitat 12 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 1.42.....	91
Figure A4.37. Habitat 13 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 1.74.....	91
Figure A4.38. Habitat 14 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 0.8.....	92
Figure A4.39. Habitat inundation estimates for the flow scenarios across the four habitats relevant for Carp life history in the Hume to Yarrawonga reach.	93
Figure A4.40. Habitat inundation estimates for the flow scenarios across the four habitats relevant for Carp life history in the Yarrawonga to Torrumbarry reach.	94
Figure A4.41. Habitat inundation estimates for the flow scenarios across the four habitats relevant for Carp life history in the Torrumbarry to Wentworth reach.	95
Figure A4.42. Habitat inundation estimates for the flow scenarios across the four habitats relevant for Carp life history in the Edward River.	96
Figure A4.43. Habitat inundation estimates for the flow scenarios across the four habitats relevant for Carp life history in the Gundagai to Hay reach.	97
Figure A4.44. Habitat inundation estimates for the flow scenarios across the four habitats relevant for Carp life history in the Hay to Balranald reach.	98

Summary

Context:

The NSW Government is developing the Reconnecting River Country Program (the program) as part of the Sustainable Diversion Limit Adjustment Mechanism (SDLAM). The program is investigating options to relax or remove some of the constraints limiting the delivery of water for the environment in the Murrumbidgee and Murray valleys. A constraint is any physical, policy or operational barrier limiting the delivery of water for the environment. These options allow for more frequent environmental flows connecting wetlands and low-level floodplains than are currently possible, improving ecological outcomes in Murrumbidgee and Murray rivers and floodplains. Should the program proceed to delivery, relaxation of these constraints and subsequent increases in wetland and floodplain-connecting river flows are expected to benefit native fish, however non-native invasive fishes such as Carp (*Cyprinus Carpio* Linnaeus) may also benefit in some circumstances.

Carp are an introduced pest species that cause major environmental damage. To investigate predicted changes in Carp populations with raised flow limits under the program, quantitative population models were constructed for three program focal zones: two in the Murray River catchment (Hume to Yarrawonga and Yarrawonga to Wakool); and one in the Murrumbidgee River catchment (Gundagai to Balranald). The three focal zones were broken into six spatial units (reaches) for population modelling to reflect the ecology of Carp: (i) Murray River from Torrumbarry to Wentworth; (ii) Murray River from Yarrawonga Weir to Torrumbarry Weir; (iii) Murray River from Hume to Yarrawonga Weir; (iv) Edward-Wakool system (Picnic Point to Wakool junction); (v) Murrumbidgee River from Hay to Balranald; and (vi) Murrumbidgee River from Gundagai to Hay.

Methods:

The Carp population model is a modification of an existing model developed for the Murray–Darling Basin Authority, previously used to predict responses to flows in the Murray River (Koehn et al. 2018). The Carp model was modified for the program via a stepwise process consisting of: (i) updating a conceptual model describing Carp ecology and life history; (ii) adapting the model to each core program area and flow scenario (Table S1); (iii) incorporating flow and habitat inundation data; and (iv) reporting and presentation of results. The flow scenarios are modelled flow time-series that capture the hydrological effects of the different flow limit options (see page 24 for more information).

Table S1. Hydrological scenarios assessed for the Carp population modelling. Values represent the daily maximum flow rates for environmental flows at select gauge locations (i.e. flow limits).

Modelled flow scenario	Murray River at Doctors Point (Albury) MLday ⁻¹	Murray River downstream Yarrawonga Weir MLday ⁻¹	Murrumbidgee (Wagga Wagga) MLday ⁻¹
Base case	25,000	15,000	22,000
Option 1	25,000	25,000	32,000
Option 2	30,000	30,000	36,000
Option 3	40,000	40,000	40,000
Option 4	40,000	45,000	NA*

* Note that when amalgamating responses across all populations to calculate the total program populations response, the 40,000 ML day⁻¹ flow scenario from the Murrumbidgee populations was added to Option 4 responses in the Murray River populations.

The area of floodplain inundated is a major input variable into the Carp model given the species' propensity to occupy and breed on inundated floodplain. A 'base case' scenario (representing a flow scenario with current conditions and constraints) for inundation was compared against four elevated flow scenarios. The flow input data consisted of 120-years of habitat inundation estimates across the flow scenarios (Table S1); these data were provided by the NSW Government. Inundation was estimated using the River Murray Floodplain and the Edward-Wakool Floodplain Inundation Models (RiM-FIM and EW-FIM; Overton et al. 2006,

Sims et al. 2014) and an in-house NSW DCCEEW inundation model (DPE 2022), as well as the Computer Aided River Management System for the Murrumbidgee River (CARM) 1D hydraulic model (DPI 2015). The updated Carp model was used to simulate 1000 replicate population trajectories under each flow scenario in each population, and summary statistics (expected minimum, mean and maximum population sizes through time) for several life-history stages (e.g. adult and early life-history stages) were extracted from these model runs.

Results:

Even though Carp did not invade the Murray–Darling Basin (MDB) until the late 1960s, we present Carp population predictions for the entire flow time series (1896–2019) to provide insight into their likely long-term population dynamics. That is, we wanted to model how Carp would have responded as a population (if they had been present) under existing (base case) and potential raised flow limits (Options 1-4) through an extensive river flow history in order to provide realistic predictions over the long-term. This hydrological record also spans periods of both higher (e.g. 1950s) and lower (e.g. Millennium Drought) flows, allowing us to contextualise program scenarios across a broad range of flow conditions.

The model predicted stable Carp populations, but with periods of population decline and increases in response to broad hydrological patterns (i.e. natural large floods and droughts). These results demonstrate that the model was sensitive to hydrological inputs and predicted large declines in Carp abundance (~20% predicted declines) during the Millennium Drought. Predicted population abundances in the southern MDB were broadly congruent with empirical observations (i.e. the model outputs reflected what was observed and recorded in the field).

The model predicted very similar Carp population outcomes (numbers of juvenile and adult Carp in the model) under different flow scenarios for all river reaches (Figure S1). This indicates that there is little predicted increase in Carp populations with the proposed increased flow limits for environmental flows under program scenarios. We highlight that there may be some short-term increases in Carp populations under specific flow events, but the long-term, average Carp population is not predicted to increase significantly under program scenarios.

Similarities in the predicted adult and juvenile population responses to a range of flow scenarios are likely due to relatively small increases in the frequency of overbank flows within the model under the differing scenarios. For example, differences in the typical area of floodplain habitat inundated (average annual maximum) between the 'base case' and the highest flow scenarios (Option 3 or 4) were generally less than 5%. Density dependent effects on recruits also likely reduced differences in predicted population responses to flow scenarios. For example, slightly higher predicted Carp recruitment under increased flow limit scenarios was suppressed by adult competition in our model construct. In other words, when Carp juveniles return to the river channel from floodplain wetlands, many will not survive due to competition over limited resources.

Model sensitivity analysis show the findings are robust under adjustments to a number of model parameters and assumptions.

Conclusions:

Two main conclusions have arisen from the work in this report and are of relevance for river managers. First, the population model predicted broad-scale population responses (increases and declines) that were driven by hydrological patterns and broadly congruent with empirical observations of Carp abundances in the southern MDB. Second, the model predicted that flow scenarios would cause no change or only small (0-3%) increases in Carp populations compared to base case conditions.

Potential future work includes:

1. Consider formal validation of the Carp population model to increase confidence in Carp model predictions. A formal validation would involve comparing population model predictions and outputs (e.g. population growth rate through time) against matched metrics calculated from empirical data collection in the field (see Todd et al. 2022 for examples of validation of population models on Golden Perch (*Macquaria ambigua* Richardson) and Murray Cod (*Maccullochella peelii* Mitchell)).

2. Consider Carp population modelling for additional flow scenarios to provide further management knowledge, including a range of future climate scenarios (i.e. with protracted periods of low/regulated flows with little floodplain inundation and protracted wet periods with frequent natural floods). Modelling such scenarios would place upper and lower bounds on predicted Carp populations, which would provide context for evaluating the more common flow scenarios and give insight into model performance at the hydrological 'book-ends'.
3. Consider additional population locations (e.g. lower Darling River, lower Murray River, major wetlands and tributaries) and the construction of a metapopulation model to enable greater insight into Carp population dynamics and potential control options.

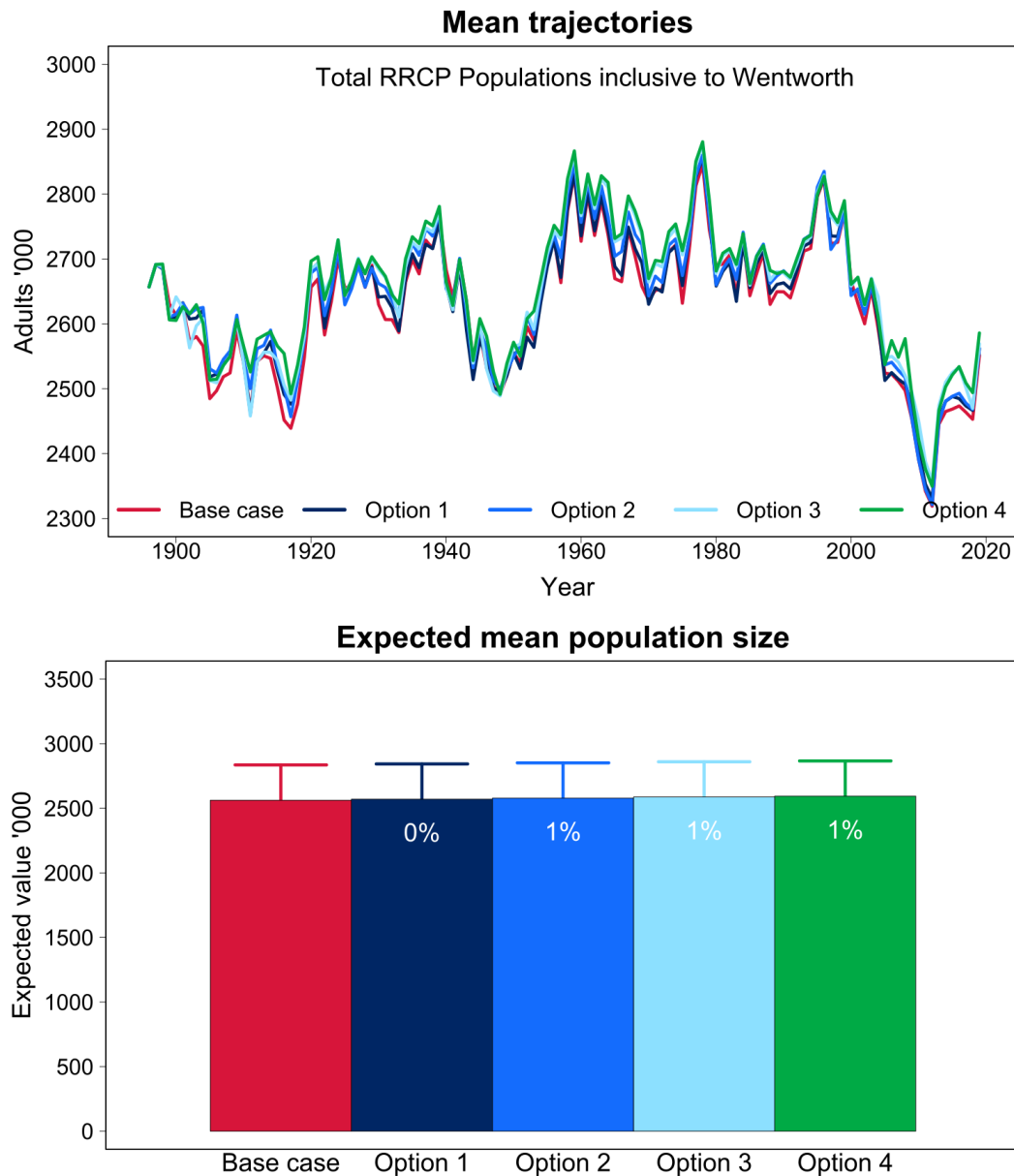


Figure S1. Modelled Carp adult population size across all modelled program reaches in the southern Murray–Darling Basin. Top panel: average adult population size; and Bottom panel: expected values of the mean population size relative to the base case, with percentage change from the base case shown in each bar. The total predicted adult population size (across all modelled populations) was relatively stable through time, with a decline starting in the late 1930s, subsequent recovery from the 1960s, and a larger decline during the Millennium Drought period (2000s). There was very little difference among the base case and higher flow scenarios in terms of predicted adult Carp populations throughout this study probably because the area of floodplain inundation was very similar among the scenarios. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

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1 Introduction

An important feature of healthy, functioning freshwater ecosystems is connectivity between rivers and their adjacent wetlands and floodplains. These connections support important ecological, hydrological, and chemical processes. However, many rivers are no longer connected with floodplains and wetlands for as often or long as would have occurred historically, and these important functions are lost or compromised. Also, many rivers are managed in the context of balancing competing human and environmental needs for water (Vörösmarty et al. 2010). Consequently, the health of many river systems has declined.

As part of the Sustainable Diversion Limit Adjustment Mechanism (SDLAM), the NSW Department of Climate Change, Energy, the Environment and Water (the department) is developing the Reconnecting River Country Program (the program) to improve river connectivity with wetlands and low-lying floodplains to support river, wetland and floodplain health. Should it proceed to delivery, the program together with other SDLAM Supply Measures would allow for more efficient use of water for the environment, thereby reducing the quantity of water needed to be recovered from other uses to achieve required environmental outcomes under the Murray–Darling Basin Plan. Under the Murray–Darling Basin Plan, a ‘constraint’ is a physical structure, policy, or operational rule that limits the volume or timing of environmental water delivery, including low-lying bridges and culverts or operational limits for river heights. Ultimately, relaxing constraints may allow improved environmental watering and outcomes.

To inform program development, the department has assessed the potential environmental benefits and risks of the flow options being considered. These assessments are part of the initial development stage of the program, which is focused on exploring impacts and benefits, assessing the benefits and costs or impacts of these options, and introducing the program to a broad range of stakeholders.

Environmental benefits assessments will provide quantitative predictions of the likely medium- to long-term ecological responses to flow scenarios (or flow limit options), using best available science, at a range of spatial scales. The outputs will help the program by:

1. informing evaluation of project flow scenarios and government decision making on the preferred flow limits in the future
2. building stakeholder and community understanding and confidence in the range of likely environmental benefits and risks of relaxing constraints
3. defining the project benefits and risks for inclusion in business cases

The program proposes works and measures projects in the Murray and Murrumbidgee rivers that are expected to have positive outcomes for native fish both in these areas and more broadly into the southern connected Murray–Darling Basin (MDB). Should the program proceed to delivery, benefits for native fish are likely as the delivery of higher flow events will provide improved connectivity with floodplains and between recruitment habitats, increase productivity and food availability, and enhance instream conditions for movement and spawning in the Murray and Murrumbidgee mainstem and floodplain anabranches and creeks.

Stochastic population modelling has been used to predict fish responses to potential future hydrological scenarios, in particular for native Murray Cod (*Maccullochella peelii* Mitchell) and Golden Perch (*Macquaria ambigua* Richardson) (Todd et al. 2022). The aim of this project was to undertake analogous modelling for the non-native and invasive Carp (*Cyprinus Carpio* Linnaeus). Carp are a major pest species and their abundance and impacts generally increase with high river flows, and floodplain inundation (Stuart and Jones 2006b; Conallin et al. 2012). Carp use inundated floodplain habitats for spawning and recruitment (Stuart and Jones 2006a), and their behaviour and feeding ecology can negatively impact upon vegetation and water quality (Koehn et al. 2000). While increases in flows are expected to benefit native fish, invasive species such as Carp may also benefit in some circumstances. Any increase in Carp numbers therefore needs to be considered alongside the predicted benefits of flow events to native fish, such as those modelled for Murray Cod and Golden Perch under the program (Todd et al. 2022). Hence, this report provides a context for evaluating Carp-mediated risks associated with different flow and floodplain inundation regimes.

The Arthur Rylah Institute for Environmental Research (ARI) has undertaken various work using population models to provide medium- to long-term quantitative predictions of Carp population responses to a range of management actions, including the provision of environmental water (Koehn et al. 2016; 2018; Todd et al. 2019; Stuart et al. 2021a). The models and approaches used in other studies can be modified and applied to the flow scenarios in the Murray and Murrumbidgee catchments. The ARI Carp population model, originally developed for the Murray–Darling Basin Authority (MDBA), will be used to investigate Carp population responses to program scenarios.

The objective of this report was to provide quantitative predictions of the likely medium- to long-term changes to Carp populations under flow scenarios in the Murray and Murrumbidgee catchments. Six river reaches were defined within three focal zones of the Murray and Murrumbidgee rivers, as relevant to evaluate modelled Carp population response to flow scenarios in this project:

1. Murray River from Yarrawonga to Torrumbarry
2. Edward-Wakool River system from Picnic Point to Wakool junction
3. Murray River from Hume to Yarrawonga
4. Murray River from Torrumbarry to Wentworth
5. Murrumbidgee River from Hay to Balranald
6. Murrumbidgee River from Gundagai to Hay.

Predictions are presented for the Murray and Murrumbidgee rivers overall, and then for each of the six reaches.

1.1 Background to population models

Population models are an important mathematical tool often used in conservation and natural resource management. ARI has developed and used population models for a variety of native fish and crustacean species to predict outcomes to management interventions at a range of spatial and temporal scales (Todd et al. 2005; 2017a; 2017b; 2018; 2020). In addition, population models have also been used to simulate population trajectories of non-native fish under a range of hydrological scenarios (Forsyth et al. 2013; Koehn et al. 2018; Brown et al. 2020; Stuart et al. 2021c).

Population models provide an immediate opportunity to explore predicted outcomes for the specified range of flow scenarios, and thus, help managers to prioritise flows that will benefit native fish communities. Quantitative predictions of fish population responses at medium- to long-term (10–50 years) temporal scales to relaxed flow constraints were made for rivers in the Murray and Murrumbidgee catchments. This includes an evaluation of relative population responses under different flow scenarios. Population models are a representation of the ‘real’ world, and hence, can also account for other major factors that influence fish populations, such as fish passage, angler harvest and cold-water pollution.

Construction of the population models relies on a collaborative approach between fish ecologists, modellers, river managers and subject-matter experts (i.e. blackwater and productivity ecologists) to collectively build an understanding of how species function and river systems operate. This provides a conceptual model, which combines the species’ ecology and management operations that inform the structure of the population models. As each management and spatio-temporal question is unique, the population models are adapted for project-specific objectives, fish species and focal zones. Model outputs can be expressed as risk outcomes, or abundances of adult or juvenile fish over biologically-relevant spatial areas and timeframes.

An important consideration when interpreting the outputs of stochastic population models is that the highest inference should be drawn from comparisons of modelled scenarios (i.e. assessing relative differences among modelled scenarios), as viewing model outcomes in absolute terms (i.e. comparing predicted total population sizes to reality) is confounded by limited understanding of true population densities and extents at this scale.

Population models can help to reduce risk and uncertainty for proposed works, especially where collecting field data is impractical. Hence, population models provide a cost-effective way to predict environmental outcomes for various proposed management regimes. Examples of the types of outputs, interpretations and implication for river operations from the modelling include:

- fish population (abundance) trajectories for each of the proposed relaxed flow constraints in the Murray, Edward-Wakool and Murrumbidgee catchments (see Figure 1 for a conceptual example) that will allow managers to compare predicted responses to each flow scenario
- outputs of different fish population measures (e.g. numbers of adults or juveniles)
- scientifically robust interpretations and explanations of results (including uncertainty, sensitivity and power analysis), and clear explanations of predicted responses to management actions
- robust and transparent evaluation of the relative population responses to the flow scenarios and hydrological recommendations that enable native fish population recovery.

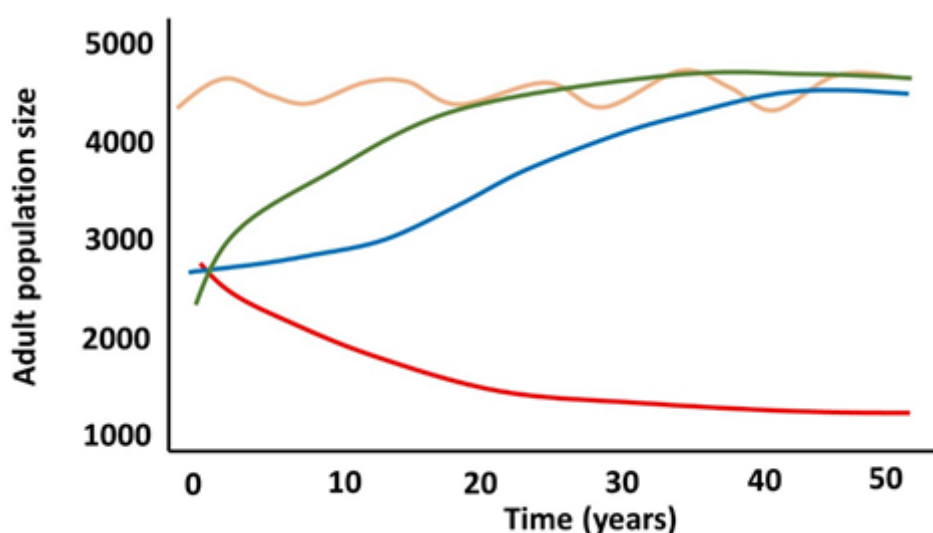


Figure 1. A conceptual example to demonstrate model outputs of population trajectories for four different management scenarios, with each coloured line representing a different management scenario (or a combination thereof). Three of the scenarios start with comparable population sizes, before one decreases (red), and the other two increase but at different rates (red and blue), whereas the size of the population stays relatively consistent through time in the fourth scenario (light brown).

For this project, stochastic population models were developed to assess the specified range of flow scenarios. Within these models, some of the parameters randomly vary to account for natural variation of the system modelled. For each scenario, 1000 iterations of the model were produced to explore the underlying variation of the model, therefore generating 1000 different population trajectories. See Figure 2–Figure 5 as examples of a single trajectory; 10 trajectories; 100 trajectories; and 1000 trajectories. The output from 1000 trajectories is summarised in Figure 6.

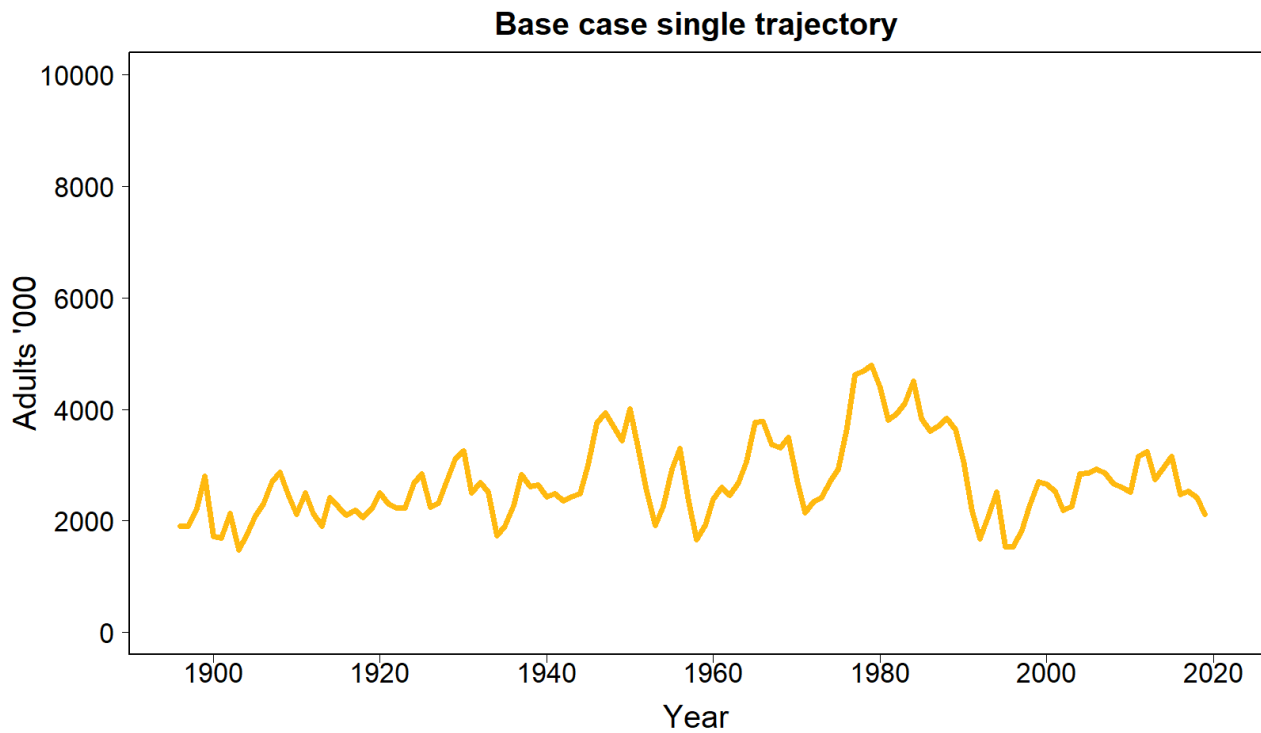


Figure 2. A single trajectory from the total program populations of Carp for the base case scenario.

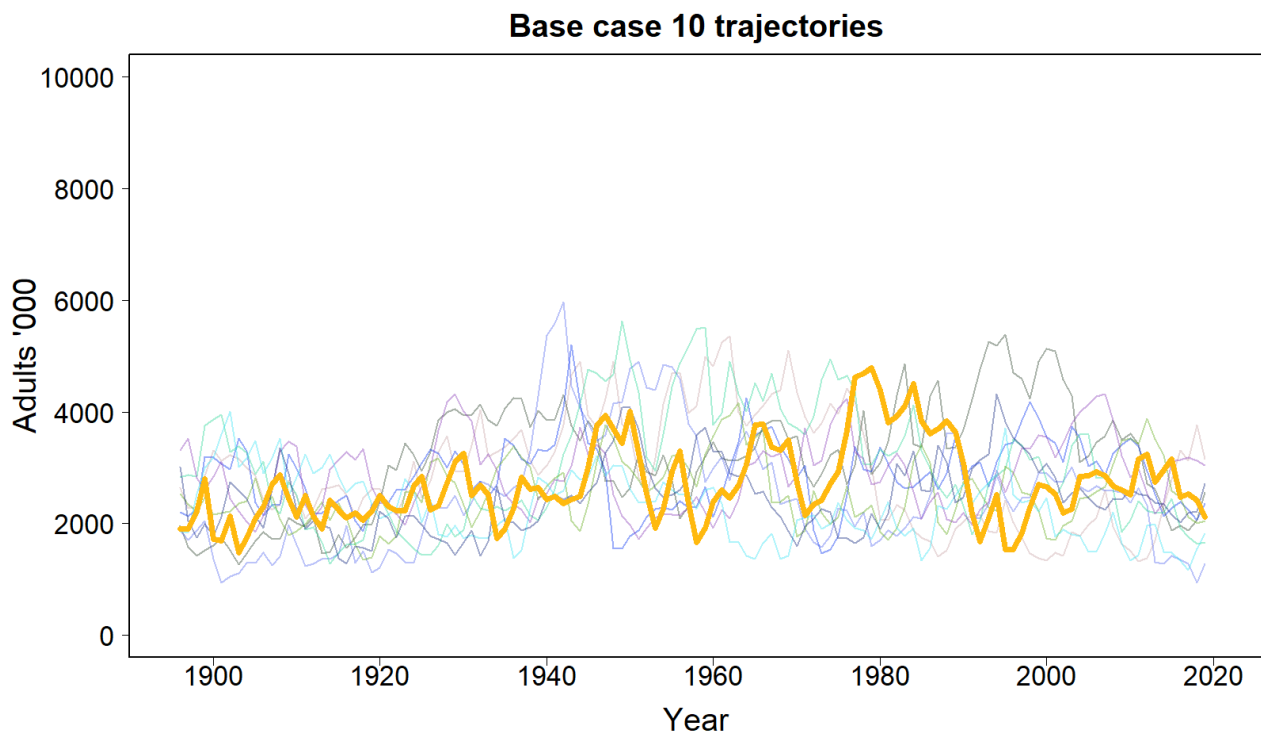


Figure 3. Ten trajectories from the total program populations of Carp for the base case scenario. The thicker yellow line represents the same trajectory as in Figure 2.

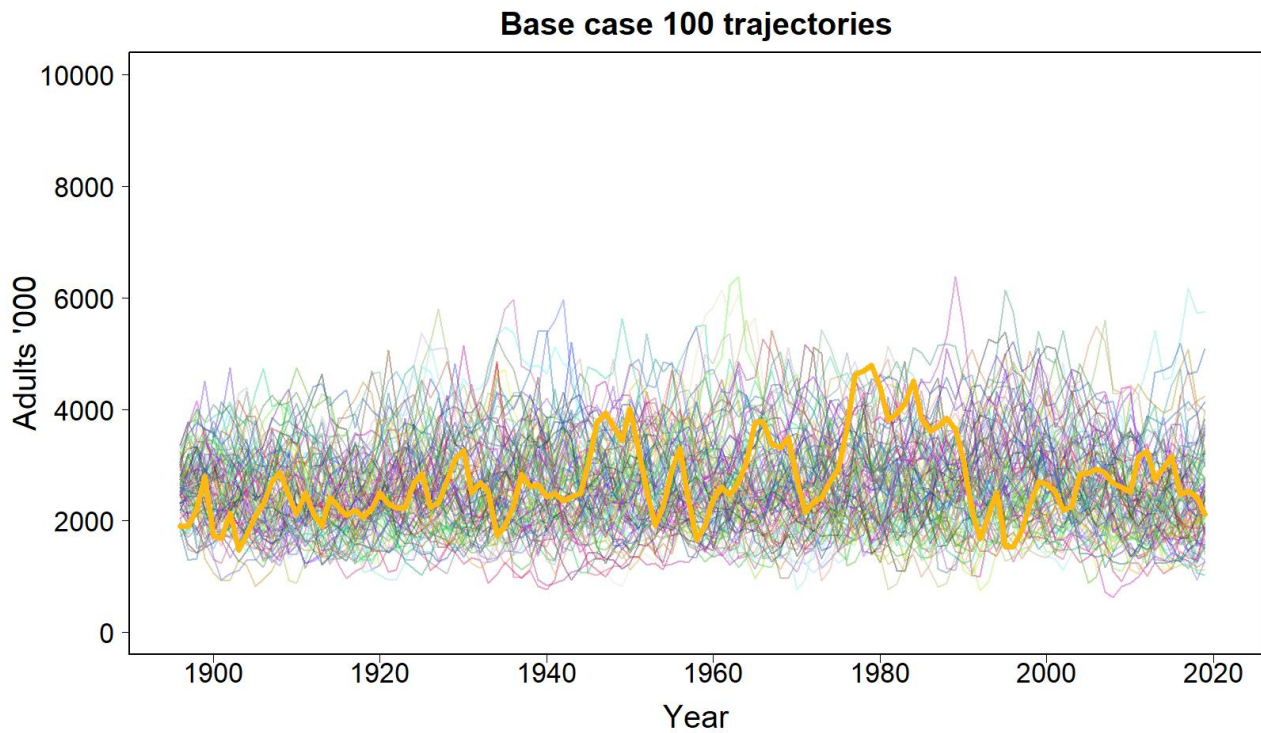


Figure 4. One hundred trajectories from the total program populations of Carp for the base case scenario. The thicker yellow line represents the same trajectory as in Figure 2.

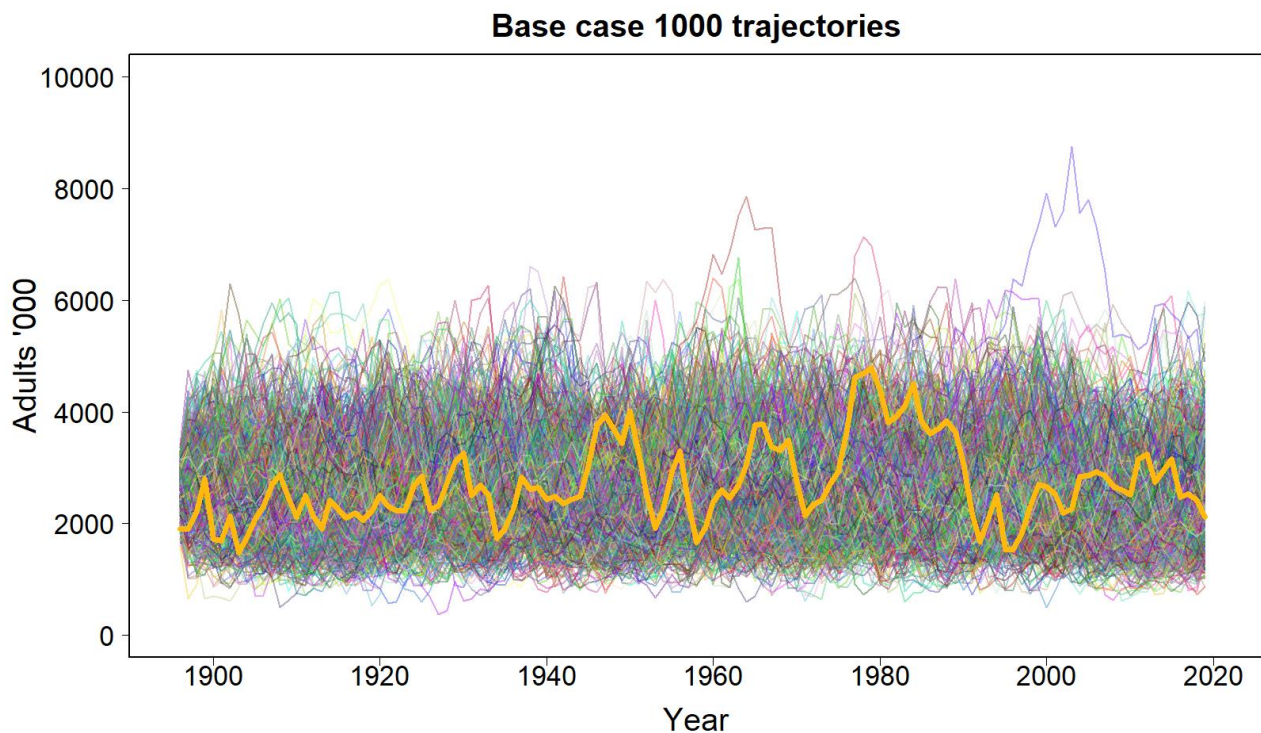


Figure 5. One thousand trajectories from the total program populations of Carp for the base case scenario. The thicker yellow line represents the same trajectory as in Figure 2.

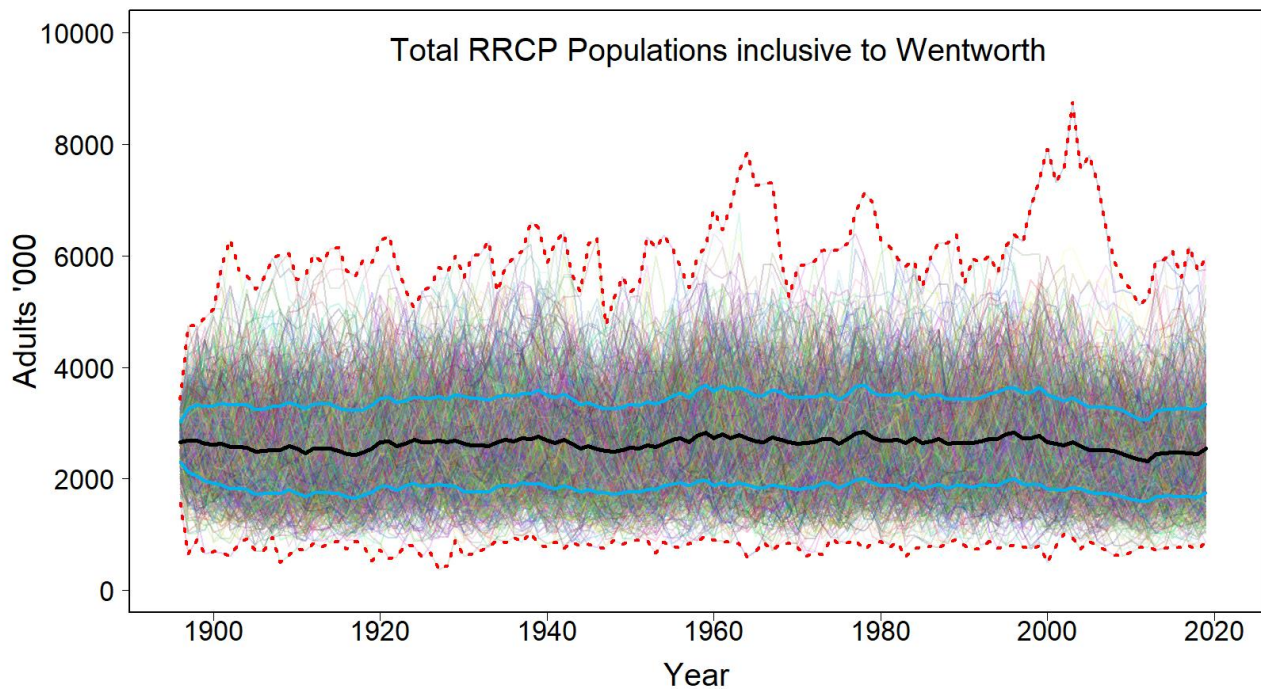


Figure 6. Summary of 1000 trajectories from the total population of Carp for the base case scenario: the black line represents the mean population size through time; the blue lines represent ± 1 standard deviation from the mean; and the red dotted lines represent the maximum and minimum levels of the trajectories through time.

To compare the base case scenario with the four flow scenarios, we present the mean trajectories of each of the five scenarios in plots (see Results). As this approach does not fully capture the variation around each of the mean trajectories, a common approach to assist in comparing different scenarios is to compile the distribution of minimum population sizes for each scenario. The minimum population size from each model run from a hydrological scenario can be recorded and converted into a cumulative distribution forming the 'distribution of minimum population sizes'. Graphing these distributions provides a visual comparison of each scenario, which transparently contrasts the likely benefits or detriments of each scenario (for a conceptual example see Figure 7 and Figure 8). Such distributions can also indicate meeting a specified threshold population size, which can be a useful comparative metric. A distribution of minimum population sizes closer to zero represents a higher likelihood that a population will have lower abundances than a population with a distribution further from zero (preferred outcome; see Figure 8). As the distribution of the minimum populations sizes is a cumulative probability distribution, it is possible to calculate the expected value (i.e. a representation of the average) of the minimum population sizes, and compare these values from different scenarios, as well as calculate the percentage change, see for example Figure 9. Finally, it is possible to examine a variety of criteria in which to partition the data, the 10% quantile population size may be used instead of the minimum population size, as well as the mean population size, or the maximum population size. See Figure 10 and Figure 12 as an example of the distribution of the mean and maximum population sizes.

Modelled outputs in the remainder of this report are summarised by presenting graphs of: (i) the mean trajectories with flow scenarios base case to Option 4 (similar to Figure 7); and (ii) bar charts of the expected mean population size with percentage change from the base case scenario, for the flow scenarios base case to Option 4 (similar to Figure 11). All other outputs are included in the appendices.

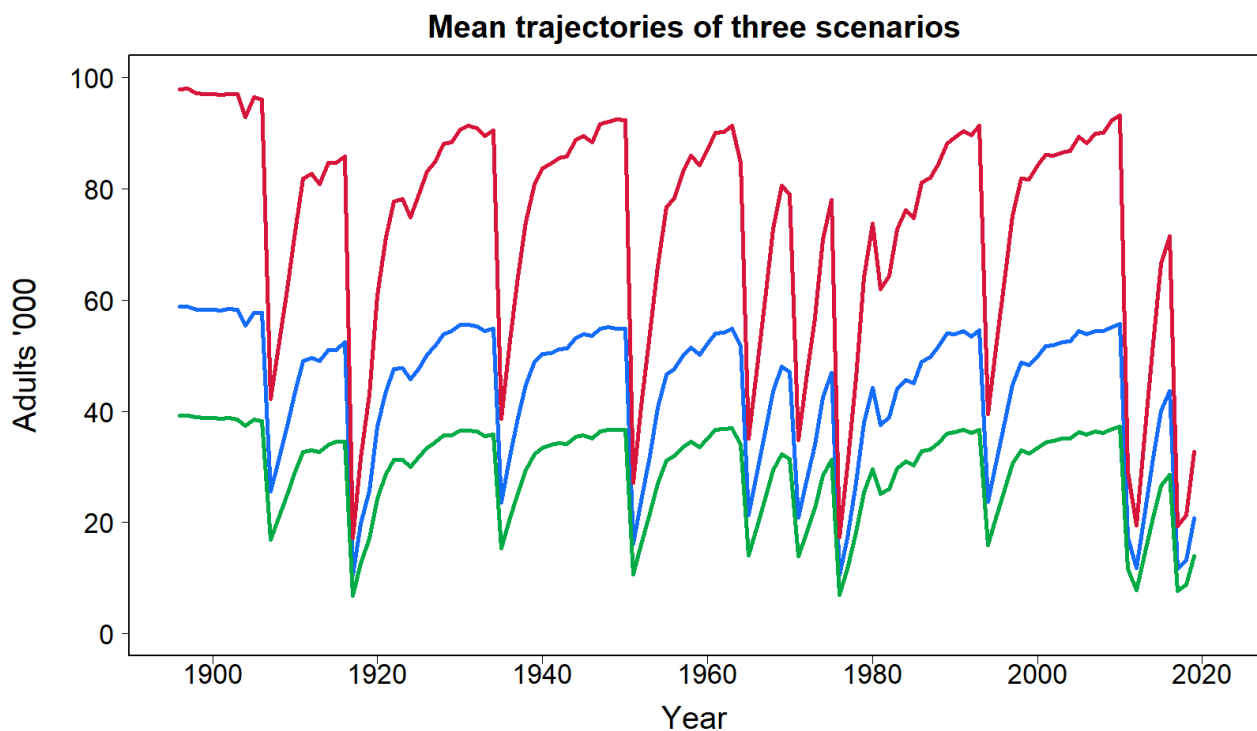


Figure 7. An example of the mean trajectories of three scenarios.

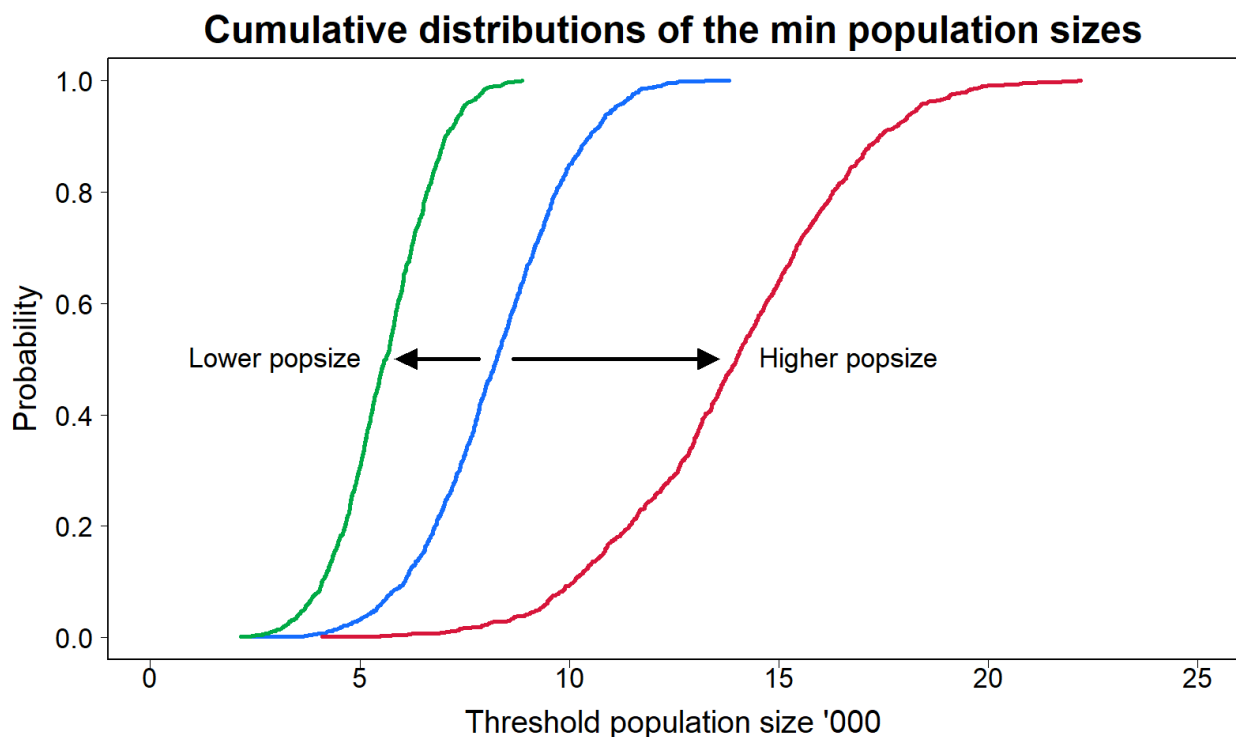


Figure 8. An example of the utility of comparing the distribution of minimum population sizes from the Figure 7 example. The green line reflects optimised management with lower numbers of Carp, the blue line reflects where the management of some threats have been addressed, and the red line reflects the poorest population outcome. These distributions represent the likelihood of the population falling below an identified threshold, with theoretical extinction occurring when this falls to zero. Key: min – minimum.

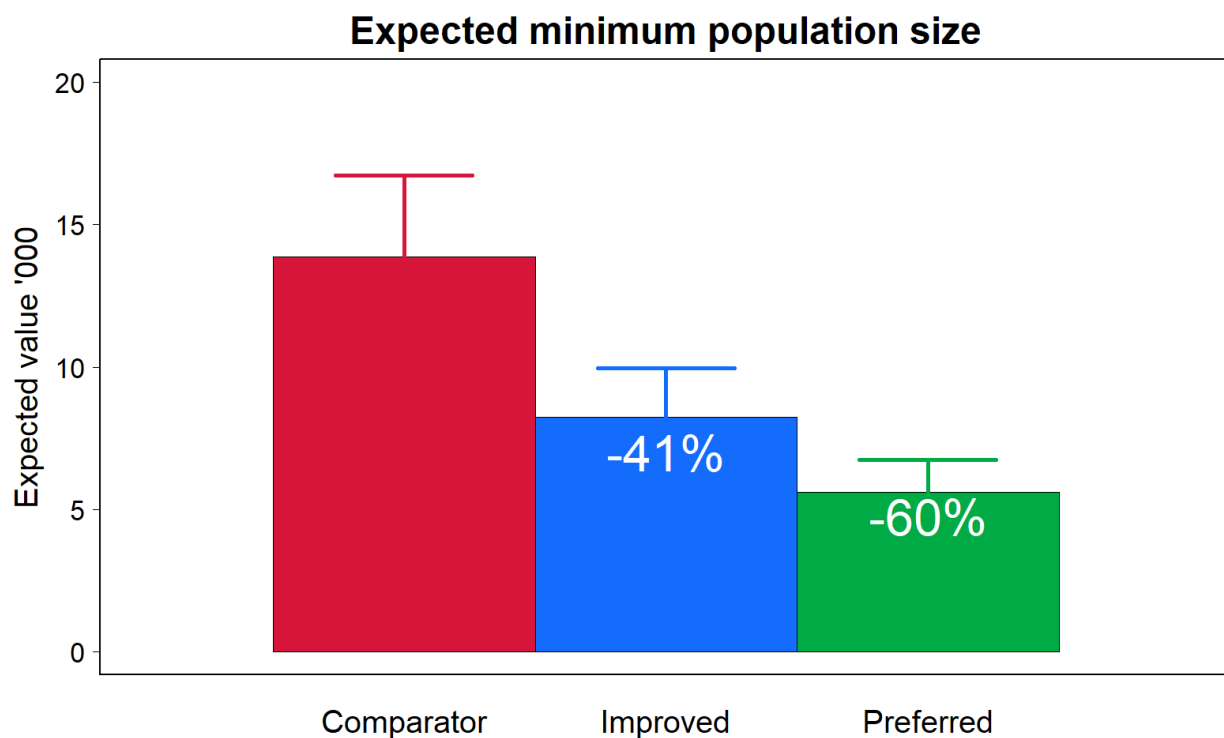


Figure 9. Bar chart of the expected minimum population size (+ 1 S.D.) from the Figure 7 example, where the percentage difference is always in reference to the expected minimum population size of the bar on the left (for model outputs this will be in comparison to the base case scenario).

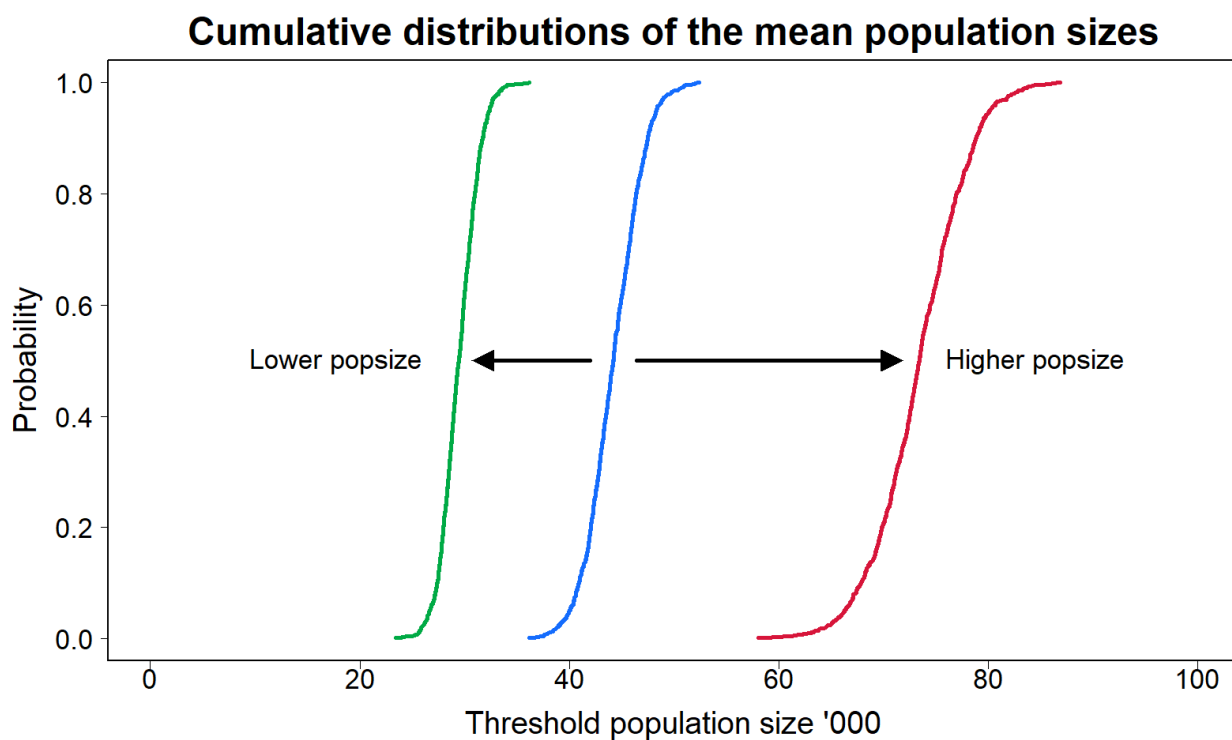


Figure 10. Indicative consequences when comparing the distribution of the mean population sizes from the Figure 7 example.

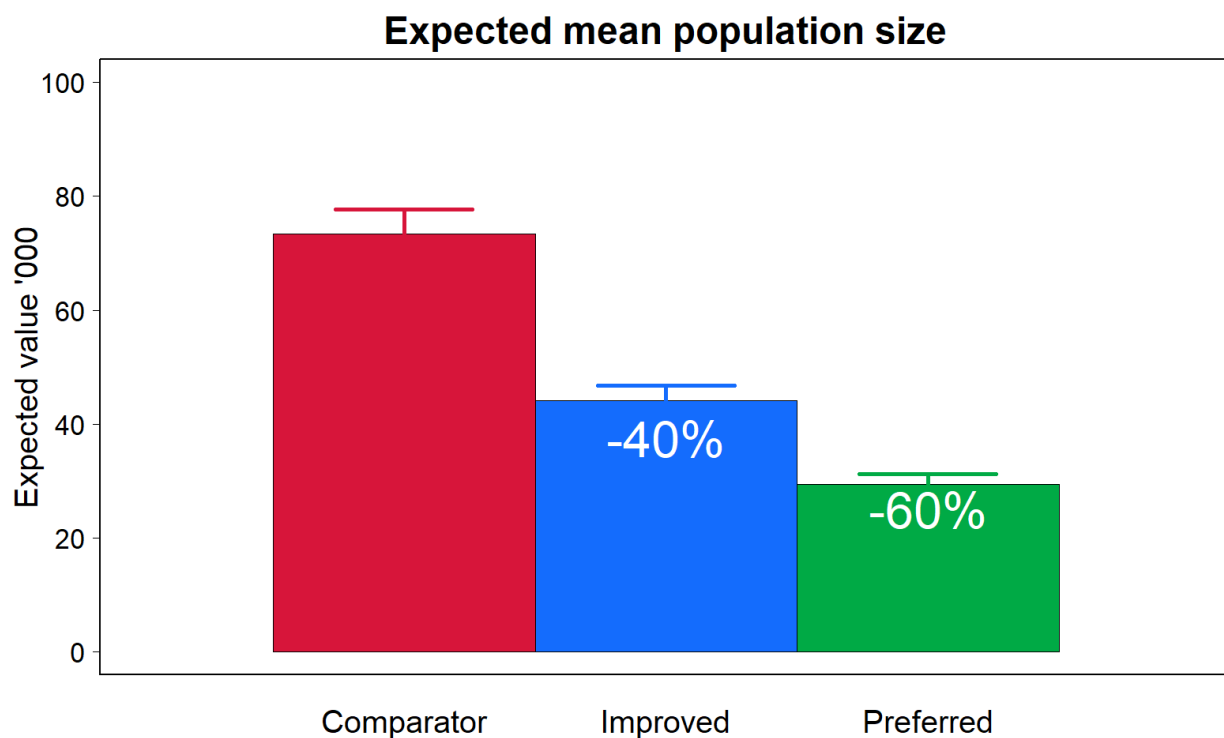


Figure 11. Bar chart of the expected mean population size (+ 1 S.D.) from the Figure 7 example, where the percentage difference is always in reference to the expected mean population size of the bar on the left.

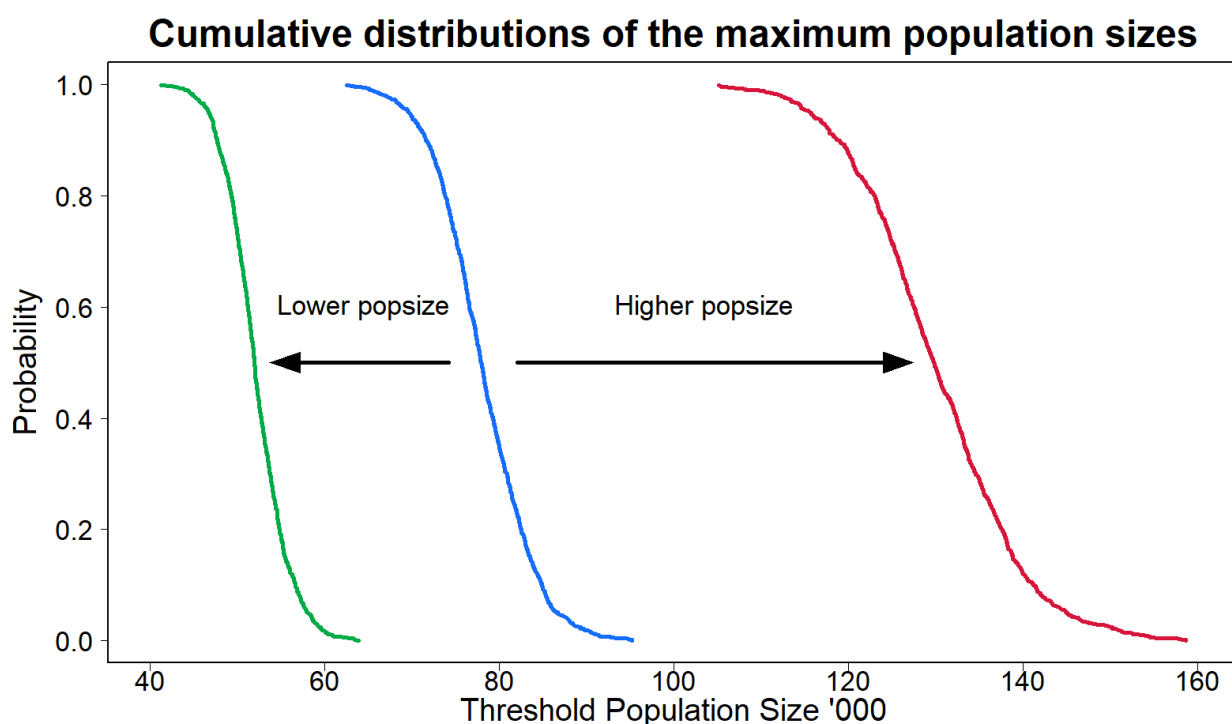


Figure 12. Indicative consequences when comparing the cumulative distribution of maximum population sizes from the Figure 7 example.

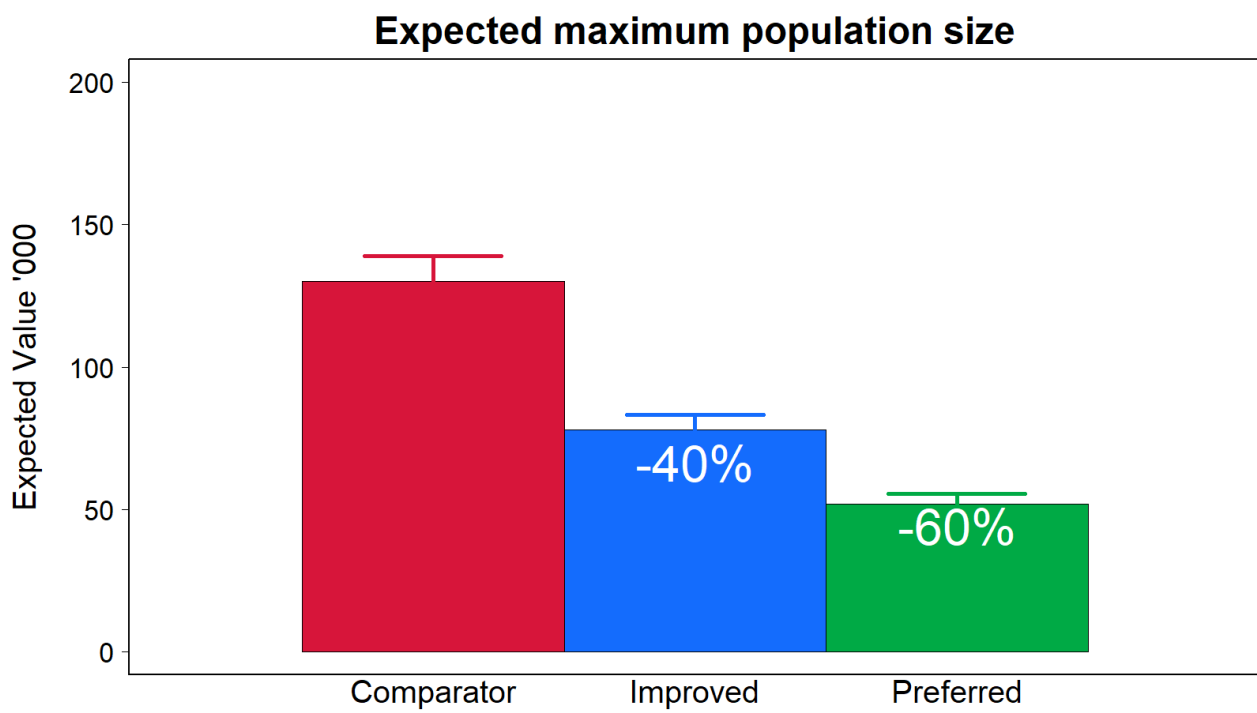


Figure 13. Bar chart of the expected maximum population size (+ 1 S.D.) from the Figure 7 example, where the percentage difference is in reference to the expected minimum population size of the bar on the left.

2 Methods

2.1 Spatial area and population units

The modelling predicts Carp population responses at a range of spatial scales to enable evaluation of likely benefits of flow scenarios within each project focal area. The three program focal zones consisted of: (i) Hume to Yarrowonga (Murray River); (ii) Yarrowonga to Wakool (Murray River); and (iii) the Murrumbidgee River. These focal zones were broken into the six reaches for population modelling to reflect the ecology of Carp in the connected Murray–Darling Basin. The spatial structure of the populations was chosen by the working group to represent areas where population dynamics occur (e.g. suitable habitats for spawning and recruitment, evidence of current populations). Population boundaries were dictated by the presence of river junctions and in many cases large barriers to movement (e.g. Hume Dam on the upper Murray River). The modelled reaches were: (i) Murray River from Torrumbarry to Wentworth; (ii) Murray River from Yarrowonga Weir to Torrumbarry Weir; (iii) Murray River from Hume to Yarrowonga Weir; (iv) Edward-Wakool system (Picnic Point to Wakool junction); (v) Murrumbidgee River from Hay to Balranald; and (vi) Murrumbidgee River from Gundagai to Hay. Each reach defined the spatial extent of separately modelled Carp populations (Figure 14).

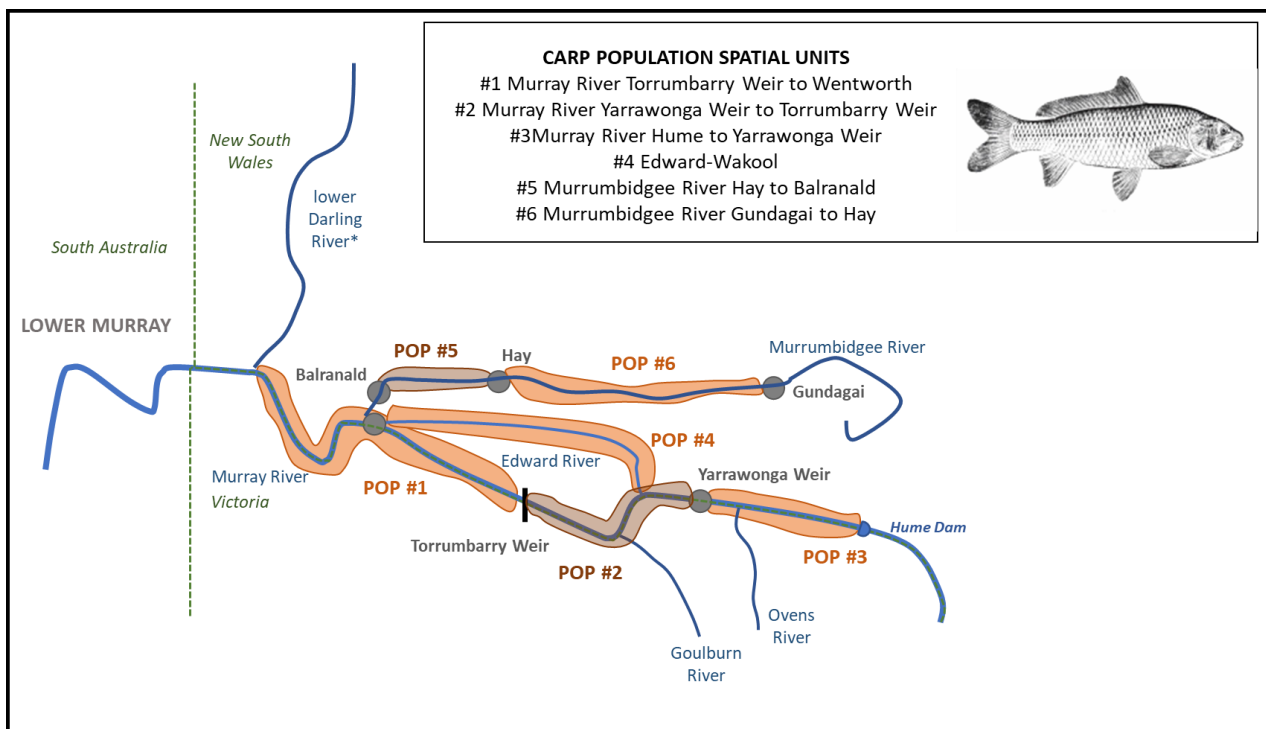


Figure 14. Spatial structure of Carp populations modelled in the Murray–Darling Basin.

2.2 Program logic

Modification of the existing Carp population model for this project followed a stepwise process consisting of: (i) defining a conceptual model of Carp life history; (ii) adapting the population model to each core program focal area and hydrological (flow) scenarios; (iii) defining and reporting the outcomes of the modelled flow scenarios; (iv) developing estimates of floodplain inundation area for the different flow scenarios; (v) providing advice to the NSW Government concerning model application, results and risks of increased Carp populations; and (vi) reporting and presentation of results.

2.3 Conceptual models

The conceptual understanding of Carp population dynamics has previously been documented (Koehn et al. 2016) and was updated for this project. To collate ecological knowledge for informing the population models, we examined published and unpublished information to review current knowledge, identify uncertainties and develop conceptual models of Carp life history. This information was updated with additional expert opinion from the project steering committee in workshops (see section 2.4), which included fish experts from across the studied focal zones, to ensure that the latest ecological knowledge was incorporated.

2.4 Ecological and operational workshops

Meetings were convened, involving the ARI project team, New South Wales Department of Climate Change, Energy, the Environment and Water (NSW DCCEEW), experts from NSW Department of Primary Industries (DPI) Fisheries, and other agencies to:

1. revise and update our understanding of the ecology of Carp within the study area, and develop the conceptual model for Carp ecology within the bounds of the study
2. assess and modify the model structure needed for flow scenarios
3. develop the rules within the model
4. agree to the hydrological scenarios to be modelled
5. establish data needs including river flows and water temperatures, and the most appropriate gauge sites for each program area
6. adjust the population model rules for any reach-specific context, such as differing habitat use patterns or processes among modelled Carp populations.

These workshops provided high-level expertise and ensured that the modelling was based on the most up-to-date Carp ecology and riverine operational knowledge.

2.5 Carp ecology

Managing Carp effectively requires that the best available knowledge and science is used (Koehn et al. 2000). This information provides the ecological context and structure for models, and parameters for use of the population model to set priorities and address issues within the management framework. Fortunately, the ecology of Carp is well-known and has previously been collated in several publications (for example Koehn et al. 2016). This information is summarised below.

2.5.1 General biology

Carp are well known for their tolerance of a wide range of temperatures, salinities and oxygen levels (Opuszynski et al. 1989; Stecyk and Farrell 2007), high degree of mobility (Koblitskaya 1977; Brown et al. 2004), omnivorous diet (Crivelli 1981), very high fecundity (Sivakumaran et al. 2003; Bajer et al. 2012), and tendency to exploit areas with highly variable environments as spawning/nursery habitat (Bajer and Sorensen 2010). Their generalist habitat requirements have allowed them to thrive in disturbed habitats (Gehrke and Harris 2001), and their adaptations to exploit shallow basins for reproduction are likely important contributors to their invasion success (Bajer and Sorensen 2010).

2.5.2 Reproductive biology

For wild Carp, sexual maturity has been recorded at a young age: ~1 year for males and 2 years for females (Swee and McCrimmon 1966; Brumley 1996; Sivakumaran et al. 2003; Brown et al. 2005; Bajer and Sorensen 2010). In the Murray River at Barmah, maturity of 50% of Carp was observed at: 307 mm FL and 1.1 years for males and 328 mm FL and 2.7 years for females (Brown et al. 2005). In the same study, maturity of 95% of Carp was observed at 379 mm FL and 1.2 years for males and 392 mm FL and 4.7 years for females. For a small proportion of fish in optimal growing conditions, maturity can even be reached at age 0+ and 230 mm FL for males and 280 mm FL for females (Brown et al. 2005). The ability of Carp to reach early maturity is common in populations in other parts of the MDB, and we note also considerable variation in the size/age at first maturity depending on local conditions.

Fecundity is the average number of eggs a female can spawn annually, and many female Carp carry over one million mature eggs (Sivakumaran et al. 2003). For Carp, fecundity is unusually complex because females are 'fractional' or 'batch' spawners, meaning they can release batches of eggs throughout the breeding season; because egg production is almost constant, it is difficult to determine fecundity in any one year. Female Carp can also develop eggs in an asynchronous manner; some fish develop their eggs early in the season and some late.

There is a clear relationship in many fishes between maternal size and greater egg size, larval hatch size and larval survival. Therefore, it is likely that the abundance of large female Carp strongly influences annual recruitment patterns (Birkeland and Dayton 2005). Large female Carp are relatively more important for egg production for two reasons: (i) larger females carry more eggs than smaller females; and (ii) larger females produce larger eggs, which may be advantageous for larval survival (Sivakumaran et al. 2003). For example, a single large (e.g. 6 kg) female Carp may release 100,000 to 220,000 eggs in a batch (Sivakumaran et al. 2003), but this is only a fraction of her total annual fecundity of 1.5 million eggs (Hume et al. 1983). A smaller (1.25 kg) female fish may carry only 80,000 eggs. Eggs may make up a maximum of 35% of the body weight for female Carp (Sivakumaran et al. 2003).

As for many aspects of Carp biology, the sex ratio of fish is variable spatially and temporally. Female Carp tend to slightly outnumber males (1.5:1) in wetlands and at riverine access areas to wetlands, but males outnumber females (2:1 to 7:1) at riverine sites further from wetlands (Stuart and Jones 2002). Observations in the lower Murray River noted a female-biased sex ratio (1.7:1; Smith 1999), while observations at Lock 1 in South Australia revealed that pre-spawning females outnumbered males (2.6:1) during the spawning season, but the female:male ratio gradually declined (to 0.6:1) by April (Conallin et al. 2008). There are also many cases of equal sex ratios (1:1) in the MDB (Brown et al. 2005).

Carp have an unusually long spawning season of up to nine months, beginning in mid-August (depending on local conditions) and finishing by April (Sivakumaran et al. 2003; Stuart and Jones 2006a). In the Lower Murray River, the spawning season may be extended further (Smith 2005), but the peak spawning period is from October to December (Smith and Walker 2004; Zampatti et al. 2011). Within a population, there are always females with ovaries close to maturation (Sivakumaran et al. 2003), and some female Carp may spawn repeatedly within a single season (Sivakumaran et al. 2003; Smith and Walker 2004; Brown et al. 2005). At Lock 1, the gonadosomatic index (ratio of gonad weight to body weight) for female Carp peaked at 19% in December before declining to 8% in April (Conallin et al. 2008).

Carp eggs mature during winter for the spring spawning season, which begins when the water temperature rises to 15–16 °C and the photoperiod is >10 h of light (Smith and Walker 2004). This enables earlier spawning times than is possible for many native fish species that prefer warmer temperatures for spawning (Koehn and O'Connor 1990; Adamek 1998; Koehn et al. 2000), and it also enables Carp to take advantage of spawning areas downstream of water storages that release cold water (Koehn 2001). Favourable conditions for spawning include a rise in water temperature (16–24 °C) (Swee and McCrimmon 1966; Crivelli 1981; Smith and Walker 2004), and there is an upper spawning threshold of 29 °C (Hume et al. 1983).

For spawning, Carp prefer shallow littoral habitats, where they lay their adhesive eggs onto submerged and emergent vegetation, but they can also spawn on a wide range of substrate types. Spawning in the main river channel is common, but Carp actively select off-stream floodplain habitats, such as the Barmah-Millewa Forest floodplain, the Macquarie Marshes, and wetlands adjacent to the Lower Murray River in South Australia (Koehn and Nicol 1998; Stuart and Jones 2006a; Gilligan et al. 2010; Conallin et al. 2012).

Carp use floodplain habitats as spawning sites and nurseries (Koblitskaya 1977; Kanitskiy 1983; King et al. 2003; Stuart and Jones 2006a). They prefer shallow, warm, well-vegetated, lentic or slow-flowing waters for spawning (Crivelli 1981; Kanitskiy 1983; Koehn et al., 2000), and although they may spawn in the absence of flooding in the Lower Murray River (Smith and Walker 2004), increased spawning and larval and juvenile abundance have been linked with floodplain inundation (King et al. 2003; Stuart and Jones 2006a; Humphries et al. 2008). These areas have very low densities of egg and larval predators due to their rapidly expanding areas and shallow depth (Bajer and Sorensen 2010) and they frequently have severely hypoxic conditions during hot and dry periods and flooding during wet seasons, reducing predatory pressure and recruitment bottlenecks (King et al. 2003; Stuart and Jones 2006a).

2.5.3 Recruitment

Recruitment is the survival of young fish to sexual maturity (1 or 2 years of age for Carp—see above). A surrogate measure of recruitment that is often used is the number of post-larval fish or juveniles detected in their first year. Each year there is variation in the number of fish that 'recruit', depending upon spawning conditions, flow and environmental conditions, and survival/mortality processes. A strong year-class or cohort can be easily tracked through the population size structure by observing the length-frequency, especially for small fish (< 100 mm long). However, the most accurate way to determine in which years recruitment has occurred is to age the fish from sectioned otoliths, thereby isolating the strong recruitment years (e.g. Crook and Gillanders 2006). Often successful Carp recruitment is associated with specific events, such as major flooding (Brown et al. 2003).

Across the MDB, 12 Carp recruitment hotspots have been identified: Mid Darling, Lower Macquarie, Wimmera, Lower Gwydir, Koondrook-Perricoota-Gunbower, Lower Border Rivers, Lower Castlereagh, Great Cumbung Swamp, Upper Wakool, Barmah-Millewa Forest, Lake Victoria-Chowilla and Lake Brewster (Gilligan et al. 2009). This study was largely undertaken during low flow conditions, and Carp also spawn at a wide range of other sites, including some that have been shown to exhibit major population explosions (see Appendix 3 for examples).

Increased Carp recruitment with floodplain inundation is well documented in the MDB (King et al. 2003; Brown et al. 2003, 2005; Stuart and Jones 2006a; Crook and Gillanders 2006; Conallin et al. 2012), with these areas providing conditions where survival of Carp larvae is high (Zampatti et al. 2011). Hatching of Carp eggs is rapid (two days at 25°C). Larvae can develop rapidly (Adamek 1998) and are tolerant to starvation (Geurden et al. 1999); however, they are extremely vulnerable to predation (King et al. 2003). Larvae and juveniles can drift from floodplains into mainstem habitats, where survival can be variable from year to year and may depend on growth rates on the floodplain (Zampatti et al. 2011). Following periods of natural and enhanced flows in the Murray River, Macdonald and Crook (2013) found that the Barmah-Millewa Forest was the major source of Carp recruits for the Murray River main channel, with increased young-of-the-year fish compared with low-flow years. Carp show a positive response to river regulation, with juveniles being more abundant in regulated rivers than in unregulated rivers, suggesting that recruitment of these species is favoured by the more stable conditions in highly regulated rivers (Gehrke and Harris 2001). As such, floodplain inundation is a crucial driver of Carp population dynamics.

2.5.4 Growth

Carp growth rates vary with geographic location, from year to year, and throughout the year (Vilizzi and Walker 1999; Brown et al. 2003). Growth is faster in the warm water temperatures of spring and summer, particularly following flooding (Hume et al. 1983). In South Australia, Carp in the Murray River grow faster and larger than those from the Barmah-Millewa Forest area—this is probably related to warmer water temperatures (Vilizzi and Walker 1999; Brown et al. 2003). Female Carp grow faster and larger than males, an adaptation for producing greater numbers of eggs (Stuart and Jones 2002; Smith 2005). However, variability in length-at-age can be high for both male and female Carp in the Barmah-Millewa Forest area (Brown et al. 2005). Larval Carp grow very rapidly, but similar to adults, growth can vary among habitats and years, with fish spawned early in the season (e.g. September) having a longer growing period in their first year than those spawned late (e.g. February; Smith 2005). A 50-day-old Carp might be 40 mm FL and weigh 1.5 g (Vilizzi 1998; Smith and Walker 2004). As most initial field confirmations of spawning and recruitment are determined from length data, this needs to be considered in relation to length–age relationships.

2.5.5 Survival

A major gap in our knowledge of Carp life history is the lack of age-specific mortality data, particularly for egg and larval stages. However, a high proportion (at least 60–80%) of eggs are assumed to be lost to fungal infection and invertebrate grazing (Smith 2005), and a natural mortality rate of 96% has been estimated for age-0 Carp on the Murray River at Barmah (Brown et al. 2005). Young-of-the-year Carp (30–150 mm FL) are assumed to be highly susceptible to piscivorous birds (e.g. Cormorants, Darters, Pelicans, Egrets and Herons) and predatory native fish (primarily Golden Perch and Murray Cod). Natural mortality rates are likely to decrease with age, and a rate of 83% has been estimated for age⁻¹ Carp at Barmah (Brown et al. 2005).

Once Carp reach 2-years-of-age and 300+ mm FL, they have few predators except large Murray Cod, Pelicans and commercial and recreational fishers (Koehn et al. 2000; Koehn 2004). Carp may also die in large numbers

during wetland drying events, and while in shallow water they are vulnerable to predators (e.g. Pelicans, Feral Pigs, Foxes, Lace Monitors and a variety of avian raptors). Stranding of Carp in wetlands is likely to disproportionately impact mature female fish, and thus may have a large impact on populations and possibly be a potential way to control Carp biomass (Brown et al. 2005; Jones and Stuart 2008). In general, few Carp show impacts from external signs of disease or distress (project team, unpublished data).

2.5.6 Ageing and longevity

In Australia, Carp commonly reach 15 years of age (Brown et al. 2004), with a maximum age of 29 years being recorded from a large female Carp (760 mm fork length (– FL); and 8.5 kg) in the mid Murray and Barmah area (Jones and Stuart 2008). Reports of larger and older individuals exist (e.g. reports of up to 34 years), but these individuals are considered rare.

2.5.7 Movements and dispersal

Carp can move large distances at any of their life stages (Jones and Stuart 2008), with adult Carp moving between riverine and floodplain habitats. Adults also move longitudinally along rivers at a local scale of a few kilometres through to hundreds of kilometres (Stuart and Jones 2006b; Koehn and Nicol 2016). Carp are common in fishways (Mallen-Cooper 1999), where a rising water temperature > 18°C cues their migrations. Juvenile Carp (from young-of-the-year) are also highly mobile, and larvae can drift considerable distances downstream from nursery habitats before dispersing, during which process they move through fishways in very large numbers (up to tens of thousands per day) (Stuart and Jones 2006b; Crook et al. 2013). In essence, Carp are a highly mobile species with attributes that allow for rapid population expansion and recolonisation (Koehn and Nicol 2016). The reproductive success of Carp is linked with its strong migratory drive to gain access to the shallow spawning habitats (Bajer and Sorensen 2010).

An adverse consequence of the Murray River fishway program is that it gives Carp an unprecedented ability to migrate freely along more than 2000 km of river. The tagging of Carp with Passive Integrated Transponders (PIT tags), together with tag readers at fishways will be important in further understanding movement patterns (Baumgartner et al. 2014). Carp movement through fishways also provides a unique opportunity for removal with devices such as the Williams' cage (Stuart et al. 2006)—at Lock 1 (Blanchetown, South Australia) ~930 tonnes of Carp were removed between 2007–2018 at up to 5.5 tonnes per day (Barry Cabot, SA Water, pers. comm.; Stuart and Conallin 2018).

2.5.8 Habitats

Within the river channel, Carp generally prefer shallower, slower-flowing habitats (< 0.20 m/s, even still water), close to the bank, and with wood higher in the water column than other large-bodied native species (Koehn and Nicol 2014). These preferences are more similar to those of Golden Perch than they are to those of Murray Cod or Trout Cod (*Maccullochella macquariensis* Cuvier). Carp are also more likely to inhabit off-channel habitats such as wetlands and billabongs than riverine habitats. Juvenile and adult fish preferentially inhabit lentic habitats; however, they have been known to also use lotic anabranch habitats (Zampatti et al. 2011). Carp are a habitat generalist, with weaker attachments to specific micro-habitats than many native fishes. Nonetheless, Carp prefer to move onto inundated floodplain habitats to spawn (see above).

2.5.9 Resistance and resilience

Carp have a high tolerance to a range of environmental variables (Koehn 2004). These 'resistance' attributes allow them to survive a wide range of environmental conditions. A further range of 'resilience' attributes (dispersal ability, distribution, abundance, reproductive capacity) allows the species to recover rapidly after difficult environmental events (e.g. drought). In an assessment of the capability of 15 fish species in south-eastern Australia to withstand drought conditions, Carp were rated both the most resistant and the most resilient (Crook et al. 2010). These attributes may also apply to other environmental conditions and are indicative of the survival abilities of this species.

2.6 Carp population model description

Conceptual models are representations of complex systems that use available data and present causal factors to show links, interactions and processes. The development of conceptual models provides an explicit synthesis of the best available biological knowledge that incorporates key ecological attributes and needs. A series of conceptual models of Carp life-history were developed and linked to form the basis of the Carp

population model presented here. These were the Carp life cycle, population dynamics and aquatic habitats, which are described below.

2.6.1 Carp life cycle

The life cycle of Carp can be simplified into five stages (Figure 15), each with specific life purposes and attributes (Table 1) that can then be used to construct the population model. These life stages will respond differently to changed conditions, prefer different habitats, and have different dispersal mechanisms.

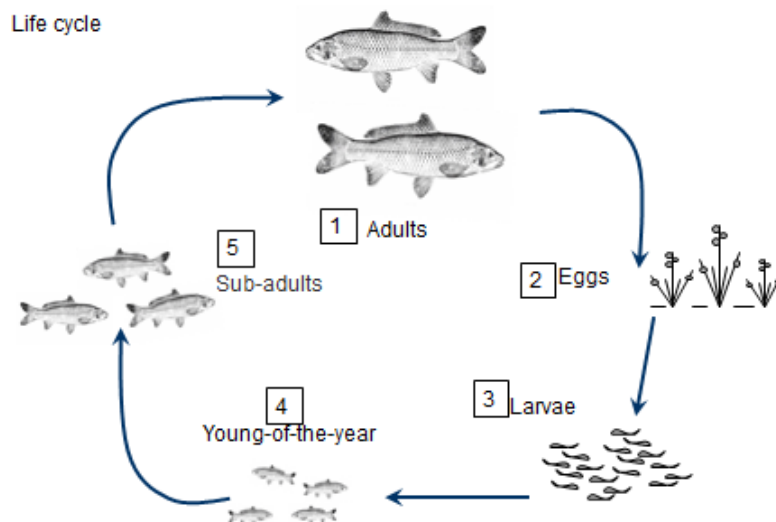


Figure 15. Schematic diagram of the various stages in the Carp life cycle. Note: young-of-the-year and subadults may both be referred to as ‘juveniles’.

Table 1. Key concepts relating to the life stages of Carp outlined in Figure 16.

Life stage	Comments
1 Adults	Occupy both flowing (river) and still-water habitats, but prefer low water velocities. Have wide environmental tolerances and are highly mobile. School and form overwintering and pre-spawning aggregations. Prefer to spawn in vegetated, shallow, still-water habitats.
2 Eggs	Attached to submerged vegetation in still, warmer water. Hatch in 2 days at 25°C.
3 Larvae	Some drift or may be flushed from slow-flowing areas. Develop rapidly.
4 Young-of-the-year	May recolonise (upstream/downstream) or drift downstream. Note: this includes ‘fingerlings’ and ‘fry’.
5 Sub-adults	May recolonise. Transition from pelagic to benthic feeding.

2.6.2 Population dynamics

Population dynamics for fish populations involves the distribution, abundance, structural, and temporal and spatial changes in relation to habitat and landscape requirements. The most important concept of populations revolves around the basic equation:

$$N_{t+1} = N_t + B_t - D_t + I_t - E_t,$$

where N = Number of fish; B = Births; D = Deaths; I = Immigration; E = Emigration; t = Time.

Other components of population dynamics are:

- Populations are often mainly reliant on the number of female fish (N_f), which indicates the actual reproductive stock.
- Fecundity (F) = the number of eggs per female.
- Total number of eggs (N_e) = FN_f
- The life stages of the species (see Figure 16a).
- Survival rates (S) between each life stage of the species.
- Recruitment, which is the replacement of an adult into the population (i.e. survival through all life stages), but survival to age 0+ is often used as a surrogate for this because the greatest mortalities occur at egg and larval stages. Note that successful spawning does not necessarily result in successful recruitment (i.e. there may be a failure of survival at the egg or larval stages).

The response of a fish population to any environmental change, such as a change in flow, will be dependent on both the initial population and the magnitude of the response initiated. If the resident population is small (as in the case of a threatened species), then the magnitude of the overall response will be low, and possibly difficult to detect. If there is no resident population (i.e. $N = 0$), then no response can be expected, even if the flow has provided the desired conditions. Conversely, a large resident population will result in a visibly large response, as is the case for many Carp populations.

To best represent Carp population dynamics in the context of this study, it was considered that the best model construct required a mechanistic understanding of the dynamics of Carp early life history, as recruitment strength drives Carp dynamics. This exploration of early life history also required an examination of the habitats utilised by Carp in this phase of their development, and the likely productivity associated with habitats. We used the life history and available data for Carp to guide the construction of a stochastic, age-based, population model with an explicit description of egg, larval, fingerling and young-of-the-year survival (Figure 16b). The stochastic age-based model allows the availability of various habitat types to drive the dynamics, and the flows determine the availability of habitat.

This construct allowed for a variety of scenarios to be considered, such as mechanistic scenarios where access to certain habitats occurs at different frequencies or specific flow-time series'. Such examination can help comprehension of the scale of Carp dynamics under natural or modified modelled flow scenarios for the likely impact on Carp dynamics and can consequently be used to inform specific flow management. The life history of Carp is well known. In general Carp are long-lived (reports exist of Carp up to 34 years old); fast-growing, attaining a maximum size of ~80 cm; exhibit variable fecundity with size; and are sexually mature by the age of 3.

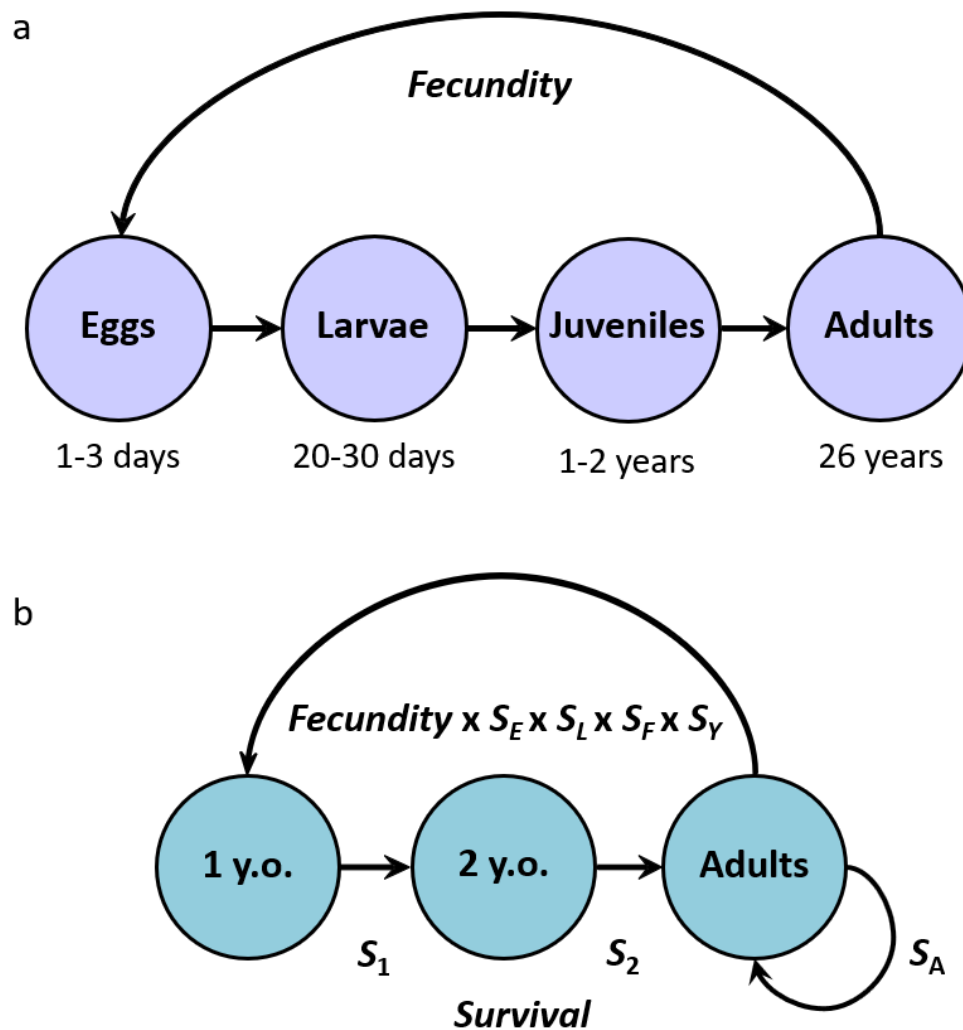


Figure 16. (a) Life history stages of female Carp with time spent in each life stage and transition to the next stage; and (b) life stages converted to an annual time step with recruitment to one year old (1 y.o.) including the early life history stages and transition from one stage/age to the next expressed as a survival rate, where S_E is egg survival; S_L is larval survival; S_F is fingerling survival; S_Y is young-of-the-year survival; S_1 is one-year-old survival; S_2 is two-year-old survival; and S_A is generalised adult survival with 26 adult age classes used in the model.

An age-structured matrix requires estimates of age-based survival rates and age-based fecundity as a function of recruitment to 1-year-olds. Age data obtained through analysing otoliths can be used to generate estimates of age-specific survival (Ricker 1975; Todd et al. 2004, 2005). An age class may be considered fully represented when the number of fish in the subsequent age class is less than the age class in question (Ricker 1975). Age data was obtained from 8634 Carp otoliths collected from around Victoria (Brown et al. 2003, Dean Gilligan NSW DPE pers. comms.). The estimated age of Carp from otolith analysis ranged from 0 to 29 years, and a curve was fitted to the resulting age data to allow age-specific survival rates to be estimated (Figure 17 and Table 2). Note that survival rates were not estimated beyond age 28 in the fitted relationship, which guided the number of age classes used in the model construct. The coefficient of variation in the survival rates was kept constant across all age classes to fully explore the variable habitat impacts on recruitment.

An age-fecundity relationship was generated from 133 aged Carp, with fecundity estimates ranging from 32,000 to 1,540,000 eggs (Brown et al. 2003). The relationship between age and fecundity varies little as age increases ($\text{Fec} = \exp(0.0051 \times \log(\text{Age}) + 13.04)$) but varies greatly within age classes (Figure 18). Assuming the distribution of eggs within a specified age to be log-normally distributed with a standard deviation of 200,000, and randomly generating fecundity given age, the resultant spread of fecundity produces a reasonable approximation of the variation in the data (Figure 19) with this relationship used to generate age specific fecundity for each time step in each iteration of the population model.

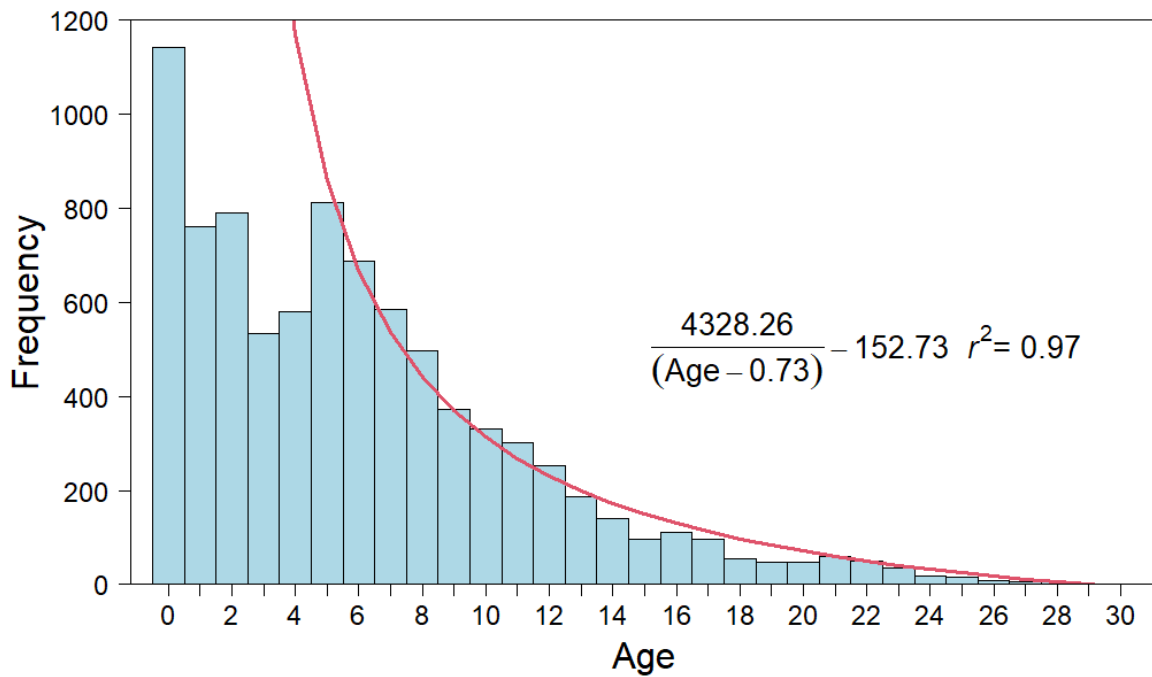


Figure 17. Carp age frequency data with curve fitted to a fully represented section of the data.

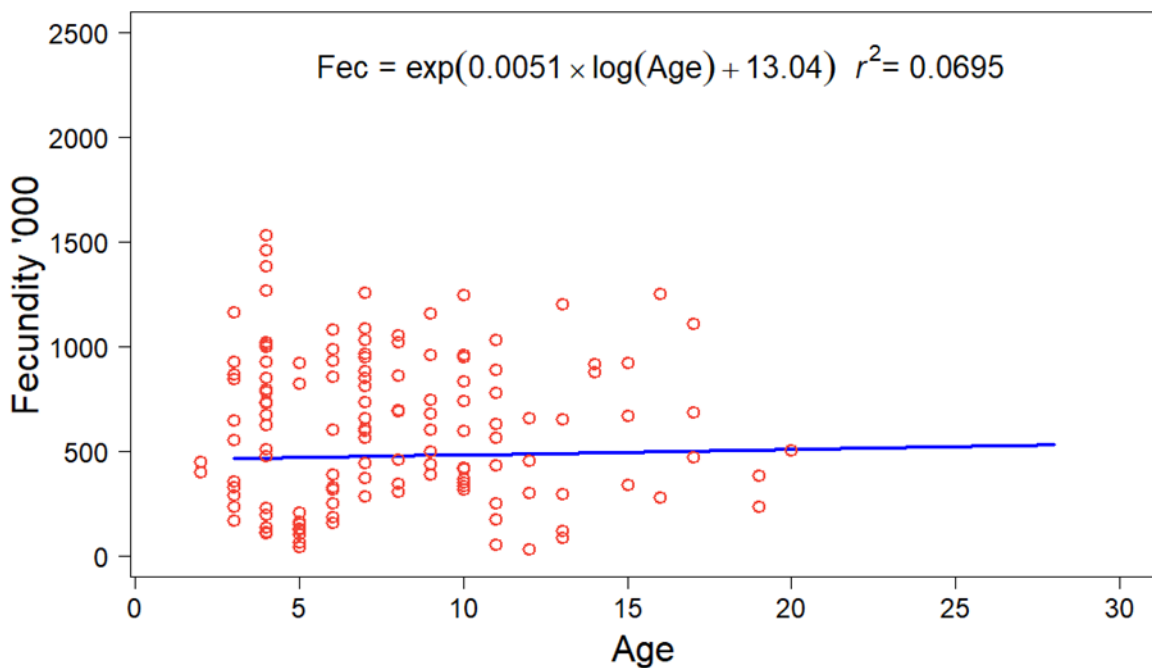


Figure 18. Carp age-fecundity data with best fitting relationship shown with the blue line. Note that variation around the estimated relationship is generated (for use as a model input) to reflect variation in the empirical age-fecundity data (see Figure 19).

Table 2. Estimated Carp survival rates and associated standard deviation (S.D.) based upon hypothesised coefficient of variation (CV).

Age	Mean survival	S.D.	CV	Age	Mean survival	S.D.	CV
1	0.20	0.02	0.1	15	0.87	0.09	0.1
2	0.54	0.05	0.1	16	0.87	0.09	0.1
3	0.67	0.07	0.1	17	0.86	0.09	0.1
4	0.74	0.07	0.1	18	0.86	0.09	0.1
5	0.78	0.08	0.1	19	0.85	0.09	0.1
6	0.80	0.08	0.1	20	0.85	0.08	0.1
7	0.82	0.08	0.1	21	0.83	0.08	0.1
8	0.84	0.08	0.1	22	0.82	0.08	0.1
9	0.85	0.08	0.1	23	0.80	0.08	0.1
10	0.86	0.09	0.1	24	0.77	0.08	0.1
11	0.86	0.09	0.1	25	0.72	0.07	0.1
12	0.86	0.09	0.1	26	0.64	0.06	0.1
13	0.87	0.09	0.1	27	0.48	0.05	0.1
14	0.87	0.09	0.1	28	0.00	0.00	0.1

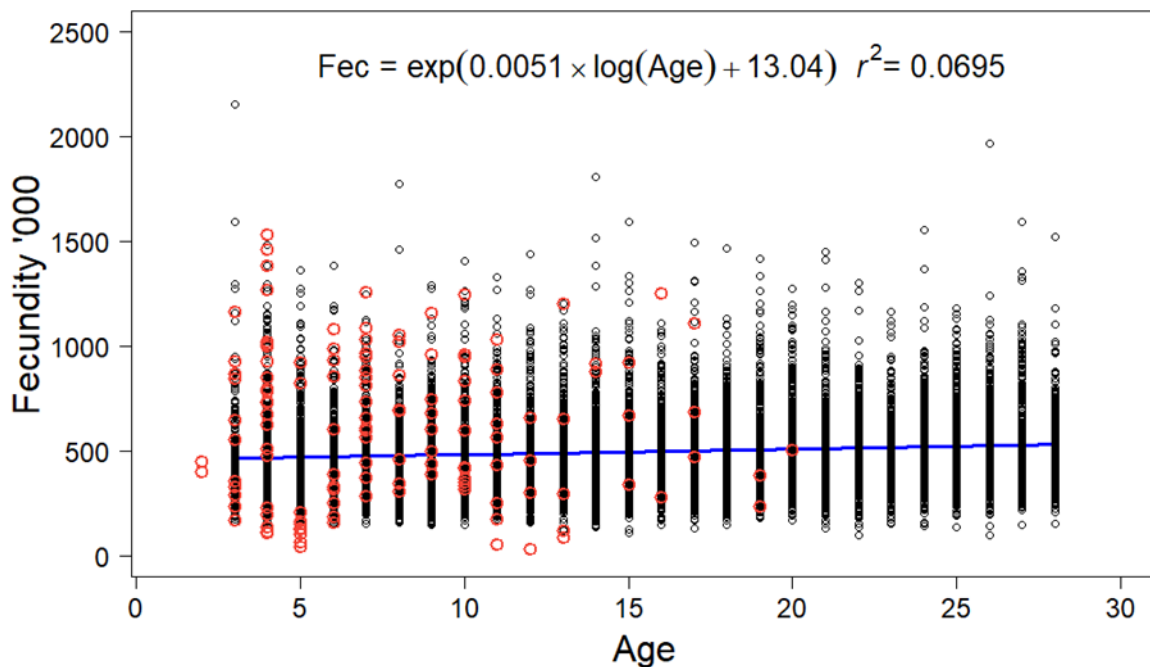


Figure 19. Generated Carp fecundity ('000s) at age. The derived age-fecundity relationship (blue line and inset equation) as shown in Figure 18 is used to generate age-fecundity model inputs (black points). Empirical age-fecundity data are again shown with red points.

The analysis of the age frequency data generated estimates of 27 survival rates, so these could be readily used in a matrix construction with 28 age classes (where the final age class was specified to be 0, indicating that no animal lives beyond the age of 28). The matrix construct is a female-only model, and it is assumed that there are enough males in any situation to fertilise all eggs from female fish. We also assume an even sex ratio across each population and habitat, as there is currently insufficient information to adequately model sex-dependent movement or habitat use. The construction of a 28-age class population model used calculated age-specific survival and fecundity rates, and estimated survival rates for eggs, larvae, fingerling, young-of-the-year and juvenile fish to complete the mathematical life cycle (Figure 20).

$$\begin{bmatrix} 0 & 0 & R_3 & R_4 & \cdots & R_{26} & R_{27} & R_{28} \\ s_1 & 0 & 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & 0 & s_3 & 0 & \cdots & 0 & 0 & 0 \\ 0 & 0 & 0 & s_4 & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \cdots & s_{26} & 0 & 0 \\ 0 & 0 & 0 & 0 & \cdots & 0 & s_{27} & 0 \end{bmatrix}$$

Figure 20. Age structured matrix model for Carp. Recruitment is in the top row and survival rates are in the subdiagonal, where recruitment to 1-year-olds is given by $R_{age} = Fec_{age} \times S_{eggs} \times S_{larvae} \times S_{flings} \times S_{yoy}$. Fec_{age} = the fecundity at a given age, S_{eggs} = eggs survival, S_{larvae} = larvae survival, S_{flings} = fingerling survival and S_{yoy} = young of year survival.

Solving the equation $(CarpModel - \lambda I) = 0$, where the *CarpModel* is the matrix specified in Figure 20, yields the underlying growth rate (or finite rate of increase) for Carp model. To solve this equation, an estimate of recruitment (R_{age}) for each age is required. Recruitment is the process of spawning, hatching, developing, growing and surviving to become a 1-year-old, and is given by:

$$R_{age} = 0.5 * Fec_{age} * S_{eggs} * S_{larvae} * S_{flings} * S_{yoy}$$

where Fec_{age} is the fecundity at a given age, S_{eggs} is egg survival, S_{larvae} is larvae survival, S_{flings} is fingerling survival and S_{yoy} is young-of-the-year survival. Assuming an even sex ratio for Carp, recruitment is halved to generate a female-only matrix model, as males are considered not to be limiting to reproduction.

2.6.3 Aquatic habitats, river flows and floodplain inundation

The original Carp model had 14 different flow-habitat types for its use across the southern connected Murray River, and these were also available for this project (Appendix 2). These habitats are available to Carp at different flow levels and occur in different locations. Each of these different habitats would yield different estimates of the early life history survival rates and the associated survival and population growth rates given in Appendix 3. Specifying the survival rates for different habitats allows the model to explore the contribution of these different habitats to Carp dynamics. Once survival rates were estimated, the associated growth rate for each habitat type could be calculated. This provided an expression of risk in terms of likely response in population dynamics from each habitat type. For this project, not all of the 14 habitat types were present or applicable. In addition, the habitat inundation data supplied from RiM-FIM and EW-FIM modelling (described in Section 2.8) were categorised into four more general ‘habitat types’, and these were aligned with the most appropriate habitats in the model (Table 3).

Table 3. RiM-FIM, EW-FIM, and CARM outputs have provided four habitat categories: ‘all other floodplain’ habitats; ‘permanent off-channel’ habitat; ‘permanent stream’ habitat, and ‘temporary waterbodies’ habitat. These habitat categories need to be aligned with those in the Carp model. We have aligned these habitats in Table 6.

RiM-FIM/EW-FIM habitat:	Habitats options in the Carp habitat model
‘Permanent stream’	H3,
‘Permanent off-channel’	H6, H9
‘Temporary waterbodies’	H8,
‘All other floodplain’	H10

Five key habitat types were selected and used for Carp scenario modelling in this project (Table 4) with the associated survival and population growth rates provided in Table 5. Any overall growth rate >1.4 potentially exhibits very strong population growth, and strong recruitment is expected from these habitat types, as is shown by the population growth rate and the expected time taken for the population to double. Note that population growth rates less than one indicate a population decline; hence, a doubling time is not applicable. The habitats used for each modelled river reach are given in Table 6, noting that the most suitable are used for each reach, and habitat types may change between different life stages. For example, larvae may be on the floodplain, but then return to the river as fingerlings and be subject to a lower survival rate.

Table 4. Description of habitat types used for Carp scenario modelling (from Koehn et al. 2016).

No.	Habitat type	Description
H3	Main channel (mid upper Murray) bankfull	70% to bankfull irrigation flow
H6	River wetland, e.g. Barmah-Millewa Forest	Adjacent low-lying wetlands (without broader floodplain inundation)
H8	Wetland ephemeral, e.g. Hattah Lakes	Off-stream wetlands, high elevation wetlands dry out if not reconnected
H9	Wetland permanently connected, e.g. adjacent weir pool	Wetlands now inundated permanently because of the weir pools follow weir pool dynamics, e.g. all unregulated weir pool wetlands in the Lower Murray
H10	Natural floodplain inundation	Broad floodplain inundation (as per high-level natural floods)

Table 5. Percentage Carp survival elicited from expert opinion and the associated growth rate for each habitat type (from Koehn et al. 2016).

Habitat	Egg survival (%)	Larval survival (%)	Fingerling survival (%)	Young-of-the-year survival (%)	Population growth rate	Population doubling time
H3	2.45	5.24	6.89	11.00	1.02	35.00
H6	12.07	10.00	21.41	15.50	2.43	0.78
H8	7.96	5.70	16.83	7.96	1.46	1.83
H9	6.45	6.54	14.84	21.12	1.78	1.20

H10	10.90	8.15	20.31	21.39	2.41	0.79
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Table 6. Habitats used for Carp modelling in each reach for flow scenarios.

River reaches	Habitats to be used for this reach
Murray River: Yarrawonga to Torrumbarry	H3, H6, H8, H10
Edward-Wakool river system: Picnic Point to Wakool junction	H3, H8, H9, H10
Murrumbidgee River: Hay to Balranald	H3, H8, H9, H10
Murray River: Hume to Yarrawonga	H3, H8, H9, H10
Murray River: Torrumbarry to Wentworth	H3, H8, H9, H10
Murrumbidgee River: Gundagai to Hay	H3, H8, H9, H10

2.7 Model construct

A 28-age class stochastic population model was constructed based on a 28-age class population matrix (Figure 20). Stochastic mechanisms were also used to capture both demographic and environmental processes, where a binomial distribution was used to model survival of larvae and adults between discrete timesteps (Todd et al. 2020), and a Poisson distribution was used to model recruitment of 1-year-olds (see Todd et al. 2020). Environmental stochasticity was incorporated by randomly varying survival and fecundity in each year (see Todd et al. 2020), and age-specific fecundity calculated by applying age-fecundity information (Figure 19).

Stochastic population modelling uses Monte Carlo simulation to sample from distributions describing variation in population parameters. The purpose is to determine how random variation, lack of knowledge, or error affects the sensitivity, performance or reliability of the predictions (Wittwer 2004). Monte Carlo simulation is categorised as a sampling method because the inputs are randomly generated from probability distributions to simulate the process of sampling from an actual population (Wittwer 2004). Including mechanistic descriptions of demographic and environmental variation in an underlying projection matrix construct produces a stochastic population model. Demographic stochasticity is modelled by incorporating variation in the survival and reproduction of individuals (Akçakaya 1991) through a binomial distribution to model the number of individuals surviving between consecutive time steps, and using a Poisson distribution to model recruitment (Todd et al. 2005). Environmental stochasticity is modelled by randomly selecting survival and fecundity rates from specified distributions at each time step (Todd and Ng 2001).

Carp populations cannot increase indefinitely, at some point resources become limited. While early life history analysis indicates that some habitats exhibit strong recruitment potential, once these recruits move into the river channel (as flows or water regimes change) they will be competing for resources with all other age classes of Carp. If space becomes limited with an increasing population, Carp must move or die. A density-dependent mechanism was used to reduce the number of fingerlings transitioning from the floodplain to the river, recognising that large numbers of Carp do not survive this process if the adult population is relatively large. Density dependence was applied to juveniles as they came off the floodplain each year at varying strengths determined by the number of adults in the population, where the number of adult Carp was compared to a 'carrying capacity' for each reach, which set the strength of density dependence on juveniles. Carrying capacities were set for each population at two Carp per linear meter of river, which was chosen as reflective of upper limits of biomass estimates (i.e. 826 kg/ha.) of Carp in the lower Murray River (Stuart et al. 2021b). For example, if the system of interest was 200 km long, then the adult-carrying capacity was set at 400,000 Carp. This rate was adjusted to one Carp per metre in the upper Murrumbidgee River population (Gundagai to Hay) to reflect the smaller size and lower Carp abundance estimates in this reach (Stuart et al. 2021b). Note that no density dependence was applied to adults because—unlike juvenile Carp, which have a relatively limited diet (i.e. are largely planktivorous before age 1) and limited ability to disperse—we believe adult Carp are not strongly limited by density due to their omnivorous scavenger life history.

2.7.1 Model runs

Models were independently run as separate populations for each program scenario (Table 7). Each model run was conducted over the temporal extent of input flow-temperature data (i.e. 1896–2019), with initial starting population size set at 95% of the model carrying capacity in each reach. Each run consisted of 1,000 iterations, where model attributes were varied as per the description of stochasticity above. The purpose of the large number of iterations was to provide sufficient sampling from the parameter distributions to allow full exploration of the variation of the distribution, and to examine the likelihood of extreme events (Ferson et al. 1989; Burgman et al. 1993). The data generated from the simulation can be represented as probability distributions (or histograms) or converted to error bars, reliability predictions, tolerance zones, and confidence intervals (Wittwer 2004).

2.8 Model inputs

2.8.1 Hydrology, gauges and inundation

The flow scenarios assessed for carp population responses are a 124-year time series of modelled daily river flows at key gauge locations in the Murray and Murrumbidgee rivers. Each scenario assumes a different flow limit option for environmental flow deliveries (see Table 4) and provides a holistic representation of potential patterns of river flows over time (flow regime). This regime includes managed environmental water deliveries up to the different flow limits as well as unregulated flows, consumptive water deliveries and other regulated system flows. Examples of two flow scenarios for the Murrumbidgee River (base case and Option 3) are shown in Figure 21.

Population model inputs were calculated using rules specific to each Carp life-history stage. Modelled flow data were used to generate the maximum area (m²) inundated for a minimum of 25 days across each year in each of four habitat types. A 25-day period was used as this broadly represents the time it takes for Carp to spawn and recruit (Koehn et al. 2000), and thus, gives the maximal area available to Carp to complete their life cycle in each habitat and year. The habitat types were main river channel, ephemeral wetland, permanent wetland and natural floodplain habitat. Inundation areas for floodplain habitats were then converted into relative proportions of the whole floodplain area, and the equivalent proportion of the adult Carp population was assigned to these habitats for spawning in that year. This effectively means that the proportional area of floodplain inundation represents the movement proportion from riverine habitats onto the floodplain in each year, where more floodplain inundation equates to more movement (i.e. the floodplain becomes more 'attractive' to Carp with higher inundation). The remaining proportion of the adult Carp population was then assigned to either the river channel or permanent off-channel habitats for spawning according to the relative inundation areas of those two habitat types in that year.

Table 7. Flow scenarios assessed for the Carp population modelling. Values represent the daily maximum flow rates for environmental flows at select gauge locations (i.e. flow limits).

Modelled flow scenario	Murray River at Doctors Point (Albury) ML day ⁻¹	Murray River downstream of Yarrawonga Weir ML day ⁻¹	Murrumbidgee at Wagga Wagga ML day ⁻¹
Base case	25,000	15,000	22,000
Option 1	25,000	25,000	32,000
Option 2	30,000	30,000	36,000
Option 3	40,000	40,000	40,000
Option 4	40,000	45,000	NA*

* Note that when amalgamating responses across all populations to calculate the total program populations response, the 40,000 ML day⁻¹ flow scenario from the Murrumbidgee populations was added to Option 4 responses in the Murray River populations.

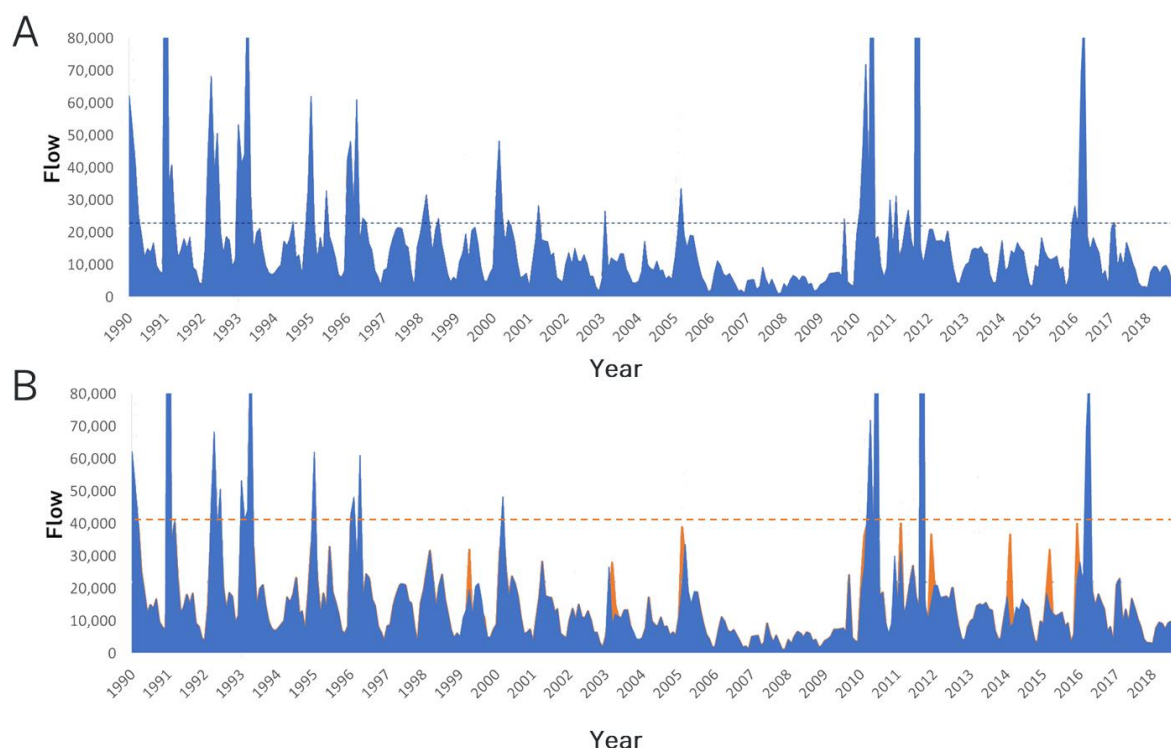


Figure 21. Modelled daily flow (in ML day⁻¹) for the Wagga Wagga gauge on the Murrumbidgee River plotted through time in years for differing program scenarios. Panel A shows flow in the blue underfilled line for the base case scenario, where the dashed line indicates the current 22,000 ML day⁻¹ flow limit at Wagga Wagga. Panel B shows the base case flow in blue again, with flow for Option 3 shown with the orange underfilled line raising above base case flows (orange line is the same as blue at other times). The orange dashed line indicates the raised flow limit for Option 3 at 40,000 ML day⁻¹ at Wagga Wagga. Note that both scenarios include unregulated flows, consumptive water deliveries, other regulated system flows and managed environmental water up to flow limits, and these data were used to generate habitat inundation estimated for this study. The differences between the blue and orange lines indicate the increased flows delivered if flow limits are relaxed from base case flow limits to Option 3 flow limits.

Proportional inundation of each habitat was used to estimate proportional access of Carp populations to each habitat type and generate estimates of life-history processes. Proportional inundation was calculated as the yearly maximum inundation extent that spanned a 25-day period in a given reach divided by the total habitat area in that reach. Proportional access of the Carp population in each year was first calculated for the floodplain habitat, and access to the remaining habitats was then calculated for the remaining fraction of the population via the relative proportional inundation among the three remaining habitats in that year. Note, that the historic flow data was modelled between 1896 and 2019, but that data series assumes current regulation and extraction rates. Moreover, the Boolarra strain of Carp did not spread until the 1960s, but we modelled their hypothetical response to the entire flow-time series (120 years) as this enabled predictions of Carp responses to a range of flow conditions over the long-term. The spatial extent of potential inundation was calculated by NSW Government for each flow scenario using the River Murray Floodplain and the Edward-Wakool Floodplain Inundation Models (Overton et al. 2006, Sims et al. 2014 and others: see Table 8), and subsequently supplied to ARI. Inundation extent estimation is further described in the DPE (2022) report.

Table 8. Population units for Carp represented as for the modelling reported in this document (Figure 15).

Population identifier	River/reach	Spatial boundary	Inundation model
#1	Mid Murray River	Torrumbarry Weir to Wentworth	RiM-FIM ¹ zones 7, 8, 9, 10, 11, 12
#2	Upper mid Murray River	Yarrawonga Weir to Torrumbarry Weir	RiM-FIM ¹ zones 2, 3, 4, 5, 6
#3	Upper Murray River	Hume Dam to Yarrawonga Weir	RiM-FIM ¹ Zone 1
#4	Edward-Wakool river system	Picnic Point to Wakool junction	EW-FIM ² zones 1, 2, 3, 3a, 4, 5, 6
#5	Lower Murrumbidgee River	Hay to Balranald	Murrumbidgee-FIM ² Zone 1 and DPE inundation model ³ Zone 2
#6	Mid Murrumbidgee River	Gundagai to Hay	Murrumbidgee zone 'CARM' ⁴

¹ – Overton et al. 2006, ² – Sims et al. 2014, ³ – DPE-EHG 2022 and ⁴ – DPI 2015.

2.9 Summary of model assumptions and limitations

Every model has inherent assumptions. It is important that these assumptions are recognised and contextualised when considering the results of any modelling project (see Discussion). For model simplicity or due to lack of information, the modelling undertaken in this study excluded some impacts known to occur in the study reaches, such as the effects of some barriers to fish passage, the use of Carp barriers or cages, and the retention of Carp on the floodplain (i.e. it was assumed all Carp would return to the river). No commercial or recreational harvest was included for Carp in this modelling project.

2.10 Sensitivity analysis

Sensitivity analysis was used to explore uncertainties in model parameterisation as well as alternative rates of floodplain access. Conventional sensitivity analysis (Cross and Beissinger 2001) of the deterministic model was used to identify parameters with disproportionate influence on population growth rates (Todd et al. 2017a, b). We used four main types of conventional sensitivity analysis (Todd et al. 2018): (1) sensitivity analysis – the rate of change in the population growth rate as a function of the input parameter, which identifies the parameters with the greatest absolute influence on population growth rate; (2) elasticity analysis – the proportional rate of change in the population growth rate as a function of the input parameter, which is useful when comparing model sensitivity to parameters specified on different scales (e.g. bounded survival parameters versus unbounded recruitment parameters); (3) reproductive value analysis – the contribution of an age class to future generations, which identifies reproductively-important age classes (see Caswell 2001 for a description of approaches 1 to 3); and (4) manual sensitivity analysis – the absolute change in population growth rate given a 10% change in an input parameter (using H3 as the template; Table 4, Table A2.1 and Table A3.1), which identifies the contribution of each parameter to the population growth rate. We plotted approaches (1) to (3) to provide a visual representation of model sensitivity and produced a table of outcomes for approach (4). Additional sensitivity analysis was undertaken (Appendix 6.4: Figure A4.25–Figure A4.38) for all habitat types in Table A2.1 and Table A3.1, treating the different habitat types as an exploration of early life history survival (ELHS) rates.

Alongside conventional sensitivity analysis, model outputs were assessed at different rates of floodplain access to determine the sensitivity of the model to assumptions about the attractiveness of inundated floodplain habitats to Carp. We used two levels of floodplain access: (1) double the movement rate (DR) at which Carp could access floodplain habitat over other available habitats (proportionally adjusted for the remaining habitats); and (2) half the movement rate (HR) at which Carp could access floodplain habitat over other available habitats (proportionally adjusted for the remaining habitats). For example, if the inundation of

floodplain habitat (H10 habitat) was 20% of the available floodplain in a reach, the halved rate (HR scenario) of movement would be 10% of adult Carp moving onto the floodplain, the standard model construct would be 20% of adult Carp moving onto the floodplain, and the doubled rate (DR scenario) would be 40% of adult Carp moving on to the floodplain. Note that the doubled rate of movement was capped at 90% of the adult Carp population, that is, not all Carp access the floodplain. The sensitivity to habitat access was assessed for four locations: Hume to Yarrawonga; Yarrawonga to Torrumbarry; Edward River; and Hay to Balranald. The average adult population size for Option 4 was compared with the base case for each of the standard access, DR and HR scenarios for the full study time period.

2.11 Population responses for the period 1990–2019

Adult and juvenile population responses to flow scenarios were extracted from model runs for the period 1990–2019. These population responses were extracted from this period and analysed independently of the rest of the dataset. This analysis was conducted on the period that encompassed the Millennium Drought and a subsequent ‘recovery’ or wet period, such that model predictions could be compared to the population responses expected to occur based on current ecological understanding. Empirical records of Carp abundance are also most complete for this period (note that Carp did not invade the MDB until the late 1960s), which enables quantitative comparisons with model predictions (see Discussion).

2.12 Presentation of population model outputs

Total adult population abundance was calculated and compared to the base case for the four flow option scenarios. Predicted mean adult population trajectories through time (1896–2019) and the expected mean population size across all years (1896–2019), as well as results presented over a selected 30-year time period (1990–2019) are presented in Section 3.1. Minimum and maximum expected population sizes for each population, as well as predicted early life-history responses and habitat inundation data (used to generate population model inputs) are presented in Appendix 4.

Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time. It should be noted though that the carp population model was run for flow scenarios in the Murray and Murrumbidgee rivers independently (i.e. the model assumes no interaction between Murray and Murrumbidgee carp populations). However, Murray and Murrumbidgee results were aggregated based on the flow scenario combinations outlined in Table 7. For example: Option 3 whole system results (Total program populations inclusive to Wentworth) reflect relaxation of flow limits to 40,000 ML day⁻¹ in the Murray and Murrumbidgee rivers.

3 Results

3.1 Population modelling for scenarios

Adult populations sizes were generally relatively stable through time in all population areas (Figure 22–Figure 30). For instance, the total Carp population across all project areas was predicted to remain between 2.2 and 2.8 million across the entire time series. There was, however, some temporal dynamism in predicted adult population sizes, with a common decline starting during the hydrological period of the late 1930s (WWII Drought) followed by a general peak in hydrological period of the 1960s, and finally a common decline during the hydrology of the Millennium Drought (e.g. the Yarrawonga to Torrumbarry and Torrumbarry to Wentworth reach populations and the Edward River population, Figure 26–Figure 28). This general pattern was reflected when predicted adult population sizes were summed across the whole study region (Figure 22) and the Murray River (Figure 23). The Hume to Yarrawonga reach population did not follow this general pattern, where general declines in the predicted adult Carp population size followed strong increases in the hydrological periods of the 1920s, late 1950s and late 1970s (Figure 25). The two Murrumbidgee River populations also had similar (but less pronounced) responses in terms of predicted adult population size to the summed overall populations, and were almost identical to each other (Figure 29 and Figure 30). Moreover, when population responses were confined to the 30-year period encompassing the hydrological years 1990–2019, there was a strong decline in the predicted adult population size starting in 1995 and continuing through the Millennium Drought period to the early 2010s (~20% decline in this period), after which there was a recovery (Figure 31).

When comparing the flow scenarios considered in this study, adult population trajectories and expected mean adult population size results were very similar (Figure 22–Figure 30). When summed across all populations, Options 2, 3 and 4 produced a predicted increase of 1% over the base case and Option 1 predicted no increase (Figure 22). Combining the Murray River populations (including the Edward River population) caused the highest flow limit option (Option 4) to increase above the base case by 2%, and the Murrumbidgee River populations showed no difference between flow scenarios (Figure 23 and Figure 24 respectively). Individual populations had very similar (small) differences among the flow scenarios considered in this study (Figure 25–Figure 30). However, slightly larger increases to predicted adult Carp abundance did occur in certain populations (e.g. a 3% increase in expected mean population size for flow limit Option 4 in the Hume to Yarrawonga and Torrumbarry to Wentworth reaches: Figure 25 and Figure 27). There was almost no difference among flow scenarios in either of the Murrumbidgee River populations (Figure 29 and Figure 30).

When finer scale temporal periods are considered (relative to study wide comparisons), larger differences between program scenarios did occur in some instances. For example, the predicted adult population size across all modelled populations was ca. 50,000 larger during periods in the 1910s and late 2010s (Figure 22). These differences were most stark during periods of lower flow when environmental flows made up relatively high proportions of total river flow contributions (e.g. the period post Millennium Drought, see Figure 33). Importantly, the higher flow scenarios also often drove slower population declines relative to lower flow scenarios (e.g. see the Hume to Yarrawonga reach, Figure 25). Moreover, quicker population responses (increases) were also often observed after periods of population decline (due to lower flows in these periods) in the higher program scenarios (e.g. see the Yarrawonga to Torrumbarry reach, Figure 26). These responses were driven by stronger recruitment under higher flow scenarios (Appendix 4). The differences seen here in shorter temporal periods across the Murray River (Figure 23, Figure 25–Figure 28) were not strongly observed in the Murrumbidgee River (Figure 24, Figure 29–Figure 30), which can be explained again by very similar hydrological patterns between program scenarios (Appendix 4).

Juvenile predicted responses largely reflected those of adults, with periods of low predicted recruitment (e.g. the 1940s hydrological period) and high predicted recruitment (e.g. hydrological periods of 1919 and the late 1950s in the total program populations response, Figure 32) preceding adult responses (i.e. low (high) predicted recruitment drove declines (increases) in predicted adult populations) across populations in this study (early life-history responses presented in Appendix 4). There was very little difference between base case and flow scenarios in early life-history responses (Figure A4.11–Figure A4.19). Notably, the Murrumbidgee River populations had relatively high recruitment throughout the hydrological period and minimal differences among flow scenarios, which explains the relatively stable population dynamics observed

in adult responses (both in terms of temporal dynamics across flow scenarios and between flow scenarios). Overall, juvenile responses demonstrate that adult population dynamics were driven by recruitment within the population model structure.

The expected minimum and maximum population sizes also predominantly reflected the responses seen for the expected mean population size for amalgamated and individual populations (Appendix 4). Here, there were only slightly elevated minimum expected population sizes for some of the modelled populations (e.g. expected minimum population size was 4% higher than the base case for Options 3 and 4 in the Torrumbarry to Wentworth reach), but otherwise these results reflected the patterns seen in the expected mean population size responses. These results show that the model did not predict any population crashes nor any significant increases (i.e. the variation among trajectories of model runs was similar among the differing flow scenarios).

Analysis of population model inputs (yearly habitat inundation estimates generated via inundation models in each population location) showed generally small differences between the base case and alternative flow scenarios (see an example comparison of modelled base case flows against Option 3 flows in the Murrumbidgee River at Wagga Wagga used to generate habitat inundation data for use in this study: Figure 21). This is further illustrated in deviance plots of yearly floodplain habitat (H10 habitat) inundation estimates of the base case scenario against flow limit Option 4 (i.e. 45,000 ML day⁻¹ flow limit at Yarrawonga Weir for the Murray River populations and 40,000 ML day⁻¹ flow limit at Wagga Wagga for the Murrumbidgee River populations), where differences in the proportional area inundated were generally less than 10% and often larger for the base case scenario (Figure 33). Note that floodplain habitat (H10 habitat) is presented here as it represents the strongest driver of Carp population dynamics (greatest early life history survival), and thus, is a key driver of population model outcomes. These similarities across flow scenarios were especially pronounced in the Murrumbidgee River populations (Figure 33). Raw habitat inundation data are presented in Appendix 4 (Figure A4.39–Figure A4.44) and show some differences between population reach areas in terms of the temporal dynamics of habitat inundation among the four relevant habitats. For example, the Torrumbarry to Wentworth and Yarrawonga to Torrumbarry reaches had relatively high and consistent floodplain inundation, often with over 10% of the floodplain inundated each year. In contrast, the Hume to Yarrawonga reach and the Edward River usually had lower floodplain inundation interspersed with large floodplain inundations in some years. Additionally, both the Murrumbidgee River populations had relatively large representations of inundation of river channel habitat in conjunction with relatively small floodplain habitat inundation through time, and starkly similar inundation schedules across flow scenarios across all four habitat types.

Adult Carp mean population trajectories and expected mean population sizes

Total populations

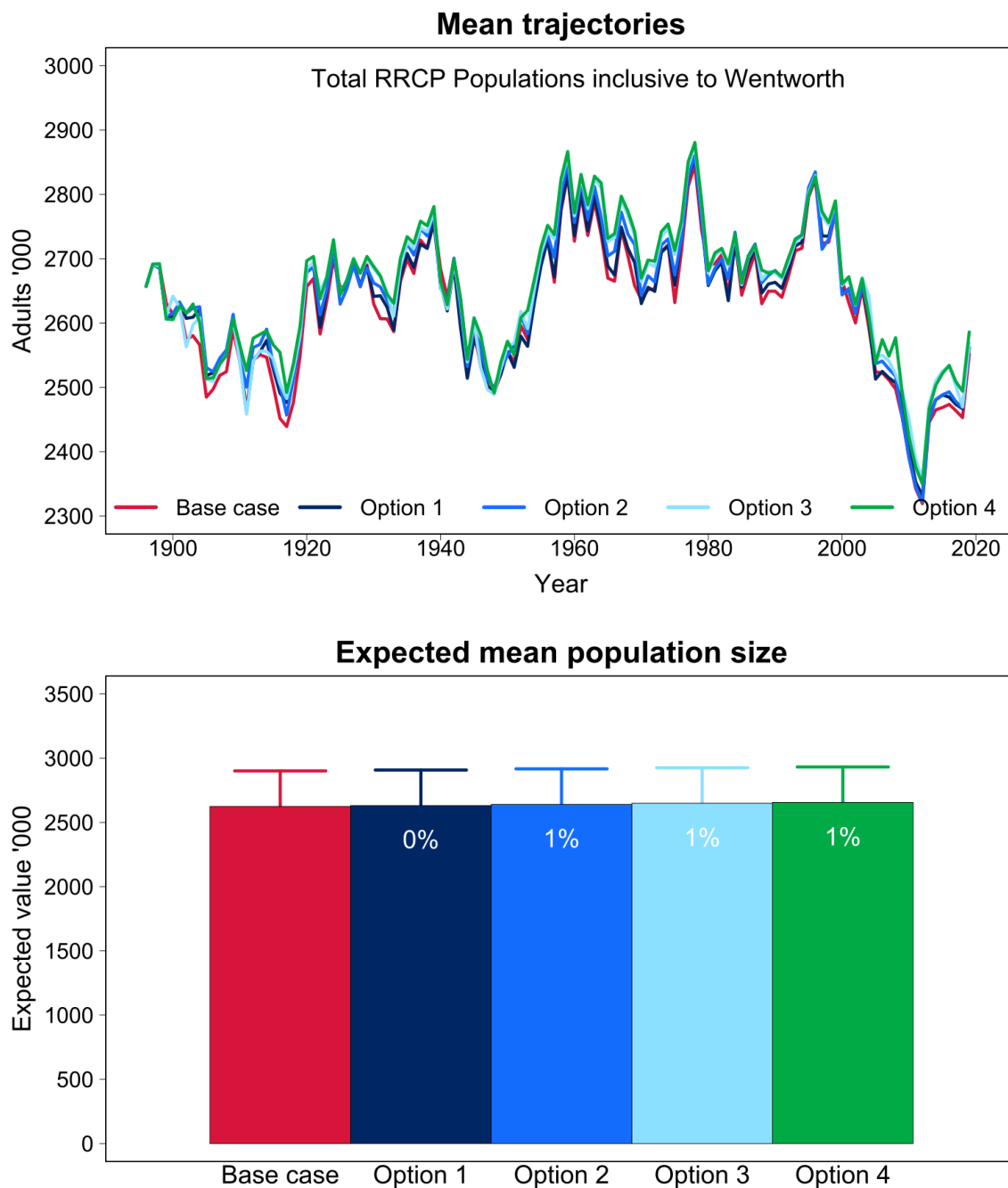


Figure 22. Modelled Carp adult population size across all modelled program reaches in the southern Murray–Darling Basin. Top panel: predicted average adult population size, and Bottom panel: expected values of the mean population size relative to the base case, with percentage change from the base case shown in each bar. The total predicted adult population size (across all modelled populations) was relatively stable through time, with a decline starting during the hydrological period of the late 1930s, subsequent recovery from the 1960s hydrological period, and a larger decline during the Millennium Drought period (2000s). There was very little difference among the base case and higher flow scenarios in terms of predicted adult Carp populations throughout this study. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Total Murray River population

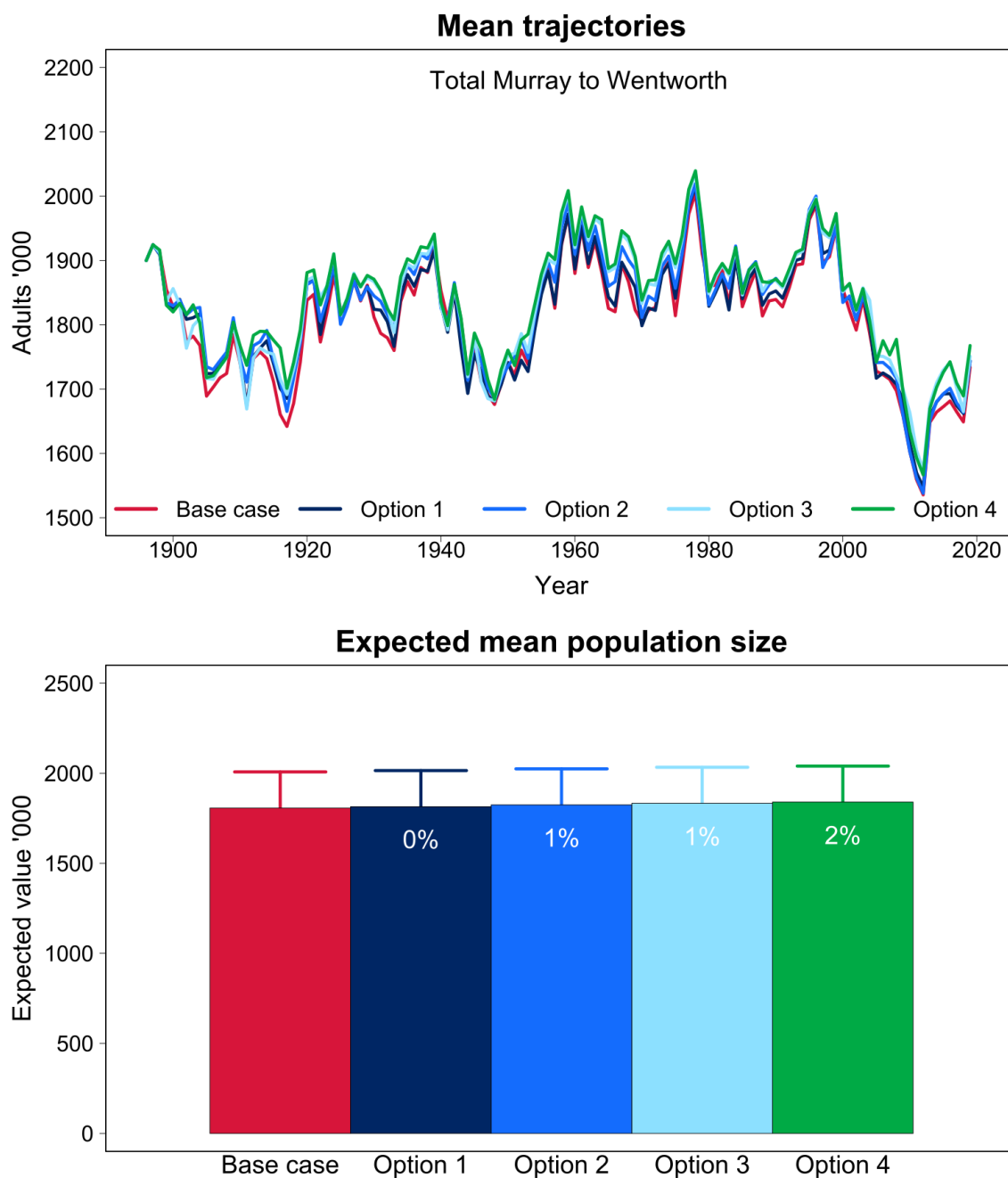


Figure 23. Modelled Carp adult population size in all reaches in the Murray River (including the Edward River). Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the base case, with percentage change from the base case shown in each bar. The total Murray River populations had largely similar temporal dynamics to the total populations, but flow limit Option 4 had a marginally larger predicted adult population size relative to the base case. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

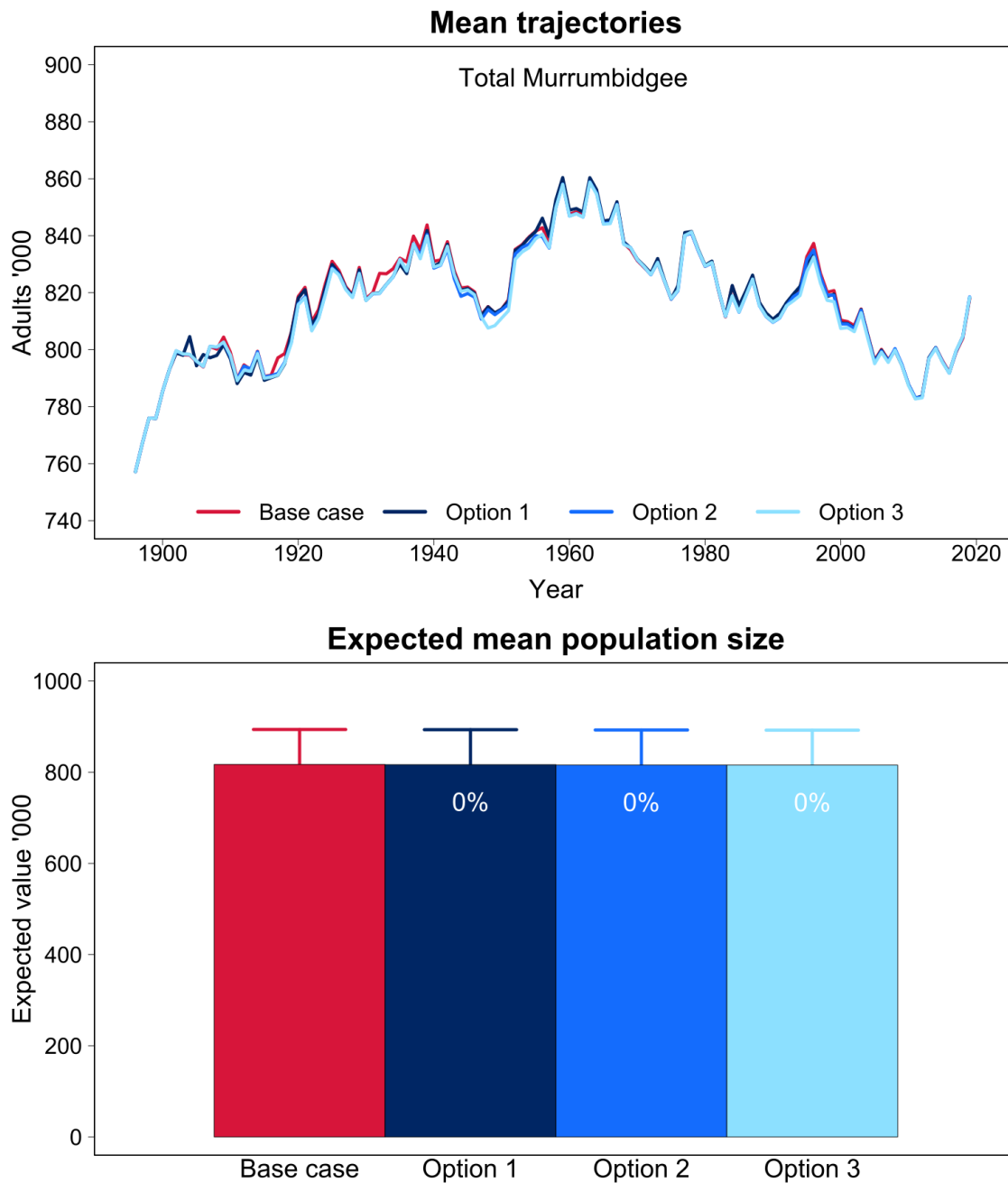


Figure 24. Modelled Carp adult population size in all reaches in the Murrumbidgee River. Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the base case, with percentage change from the base case shown in each bar. Murrumbidgee River adult populations were generally stable through time with a slight but consistent decline during the hydrology of the 1960s, and there was no difference in the expected mean population size among flow scenarios. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Individual reach populations

Hume to Yarrawonga population

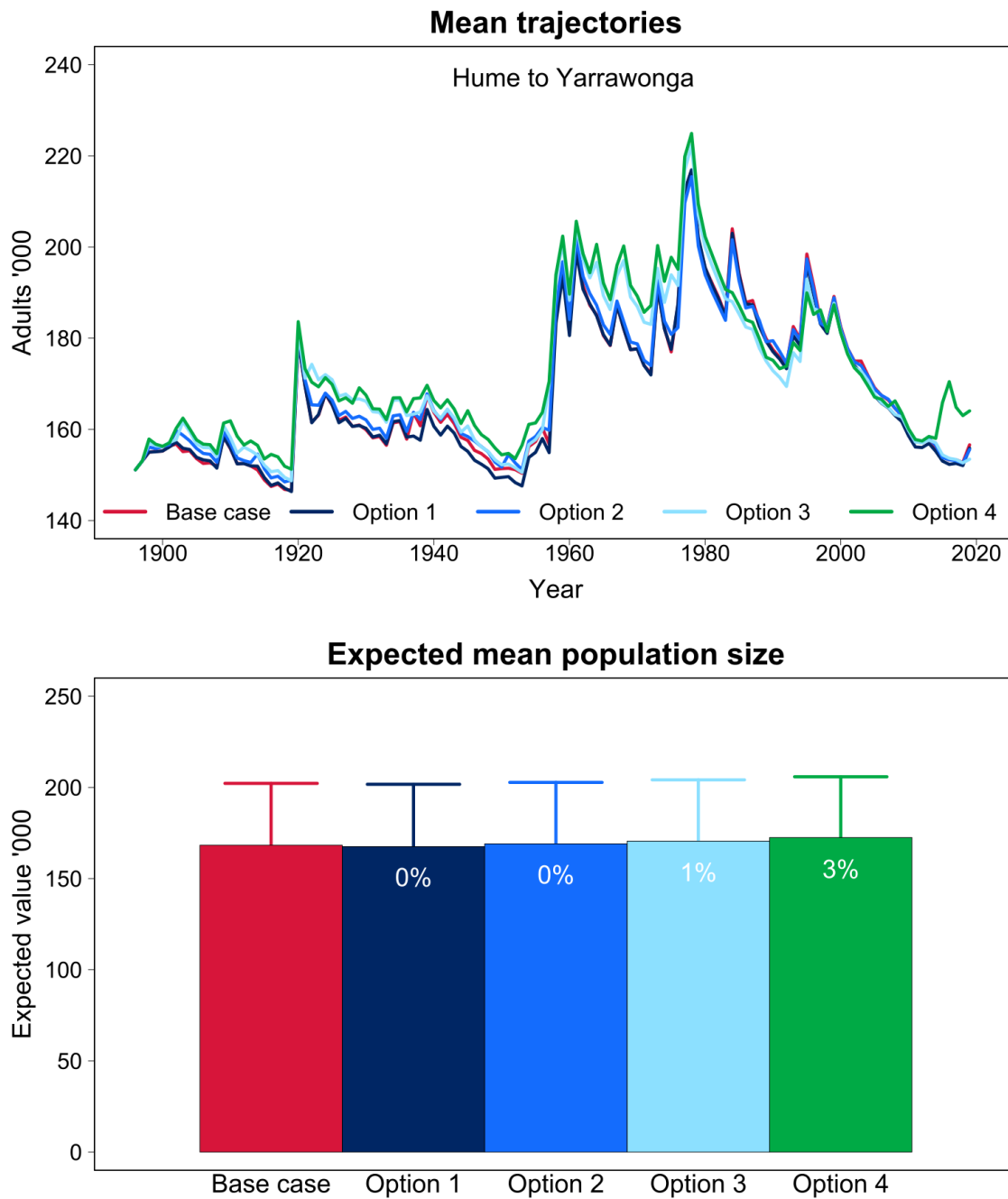


Figure 25. Modelled Carp adult population size in the Hume to Yarrawonga reach (Murray River). Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Yarrawonga to Torrumbarry population

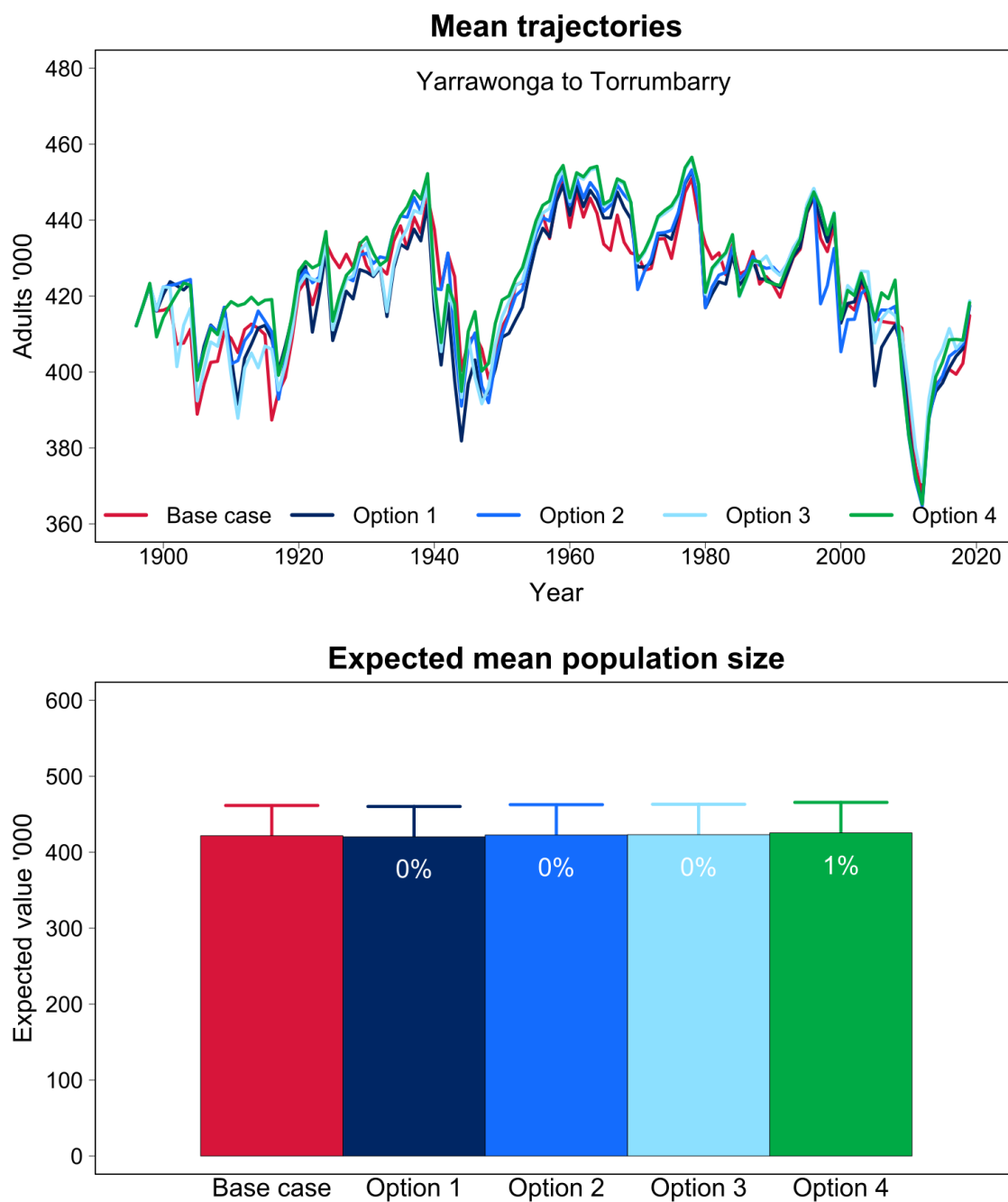


Figure 26. Modelled Carp adult population size in the Yarrawonga to Torrumbarry reach (Murray River). Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Torrumbarry to Wentworth population

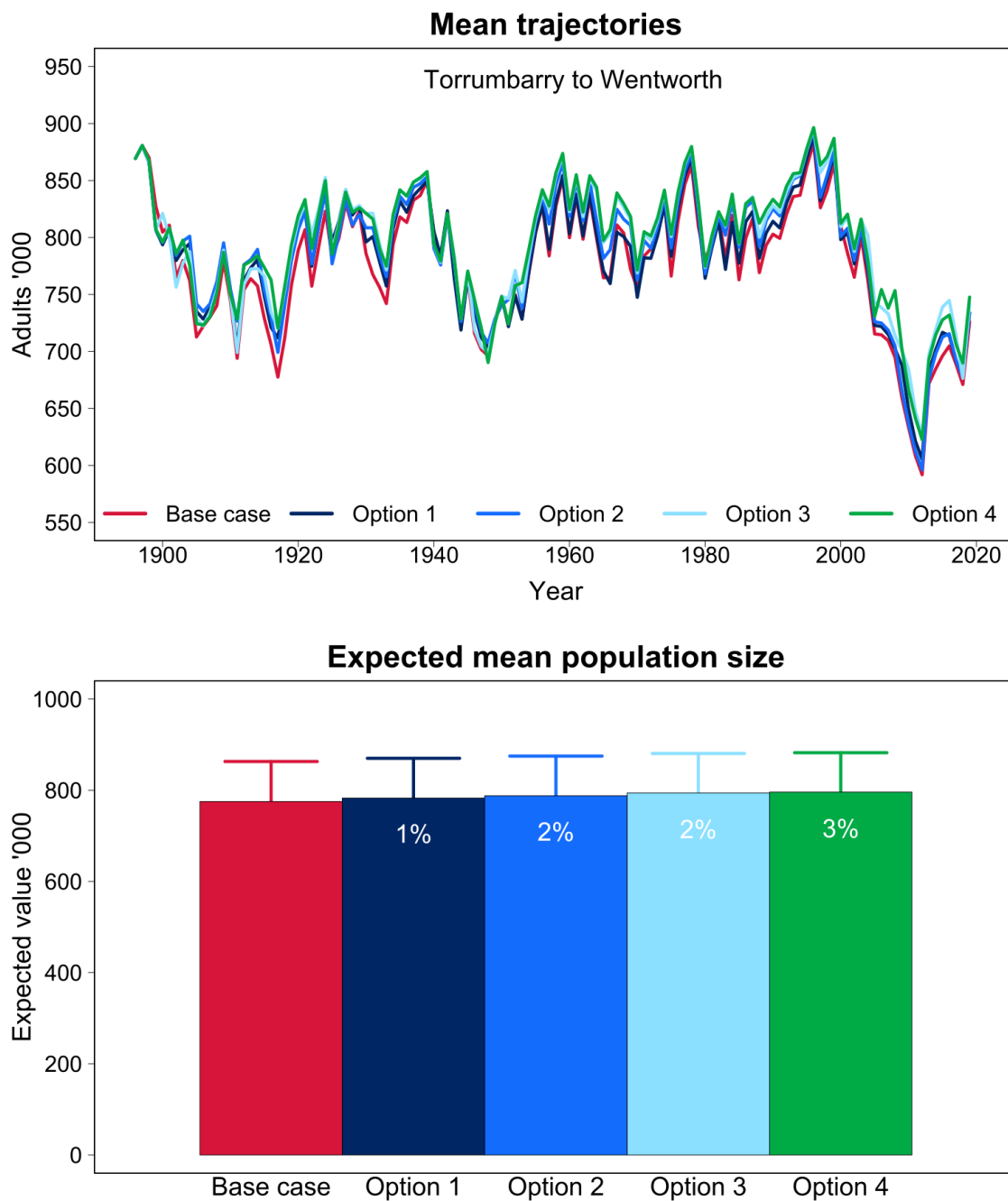


Figure 27. Modelled Carp adult population size in the Torrumbarry to Wentworth reach (Murray River). Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Edward River population

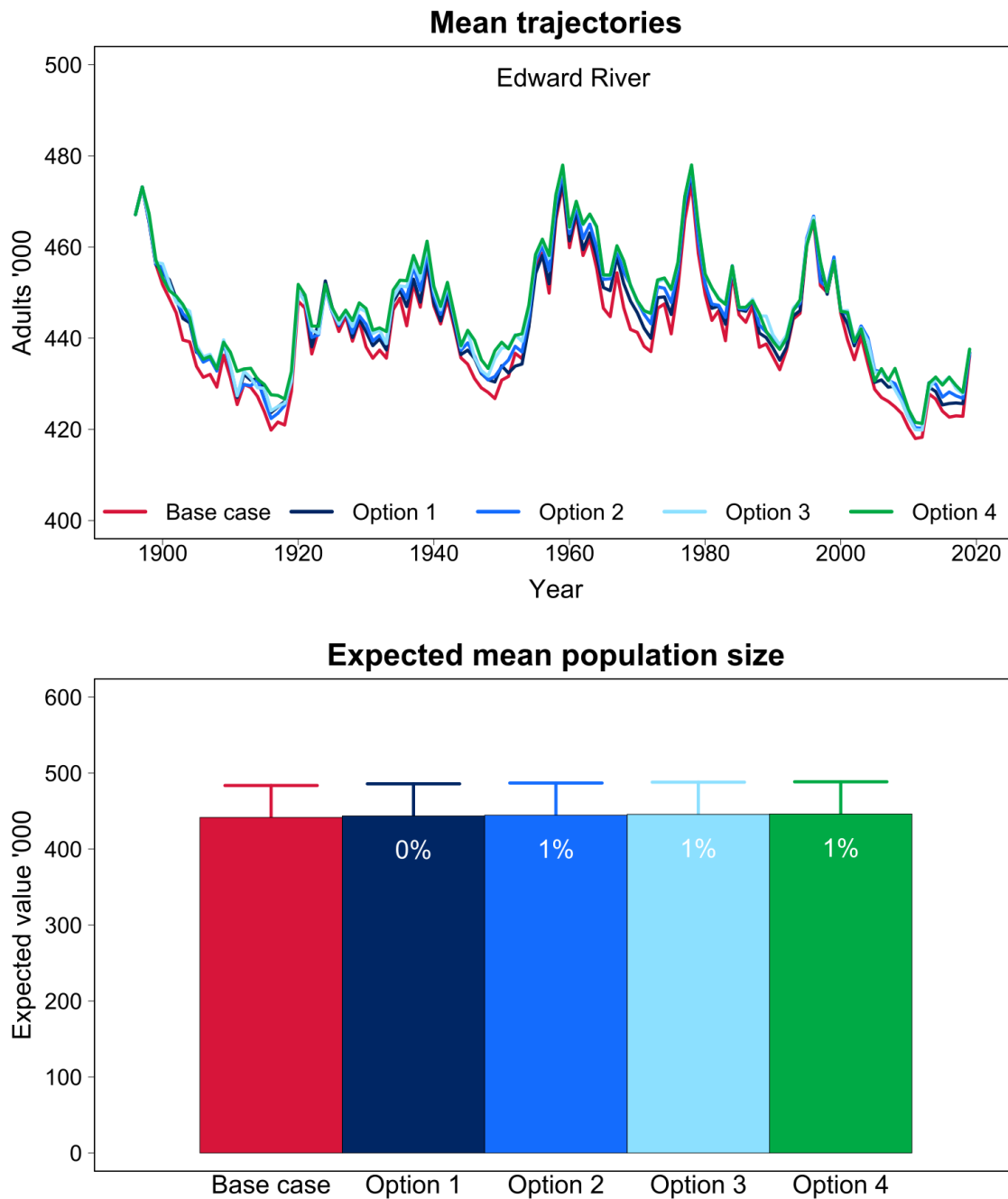


Figure 28. Modelled Carp adult population size in the Edward River. Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Gundagai to Hay population

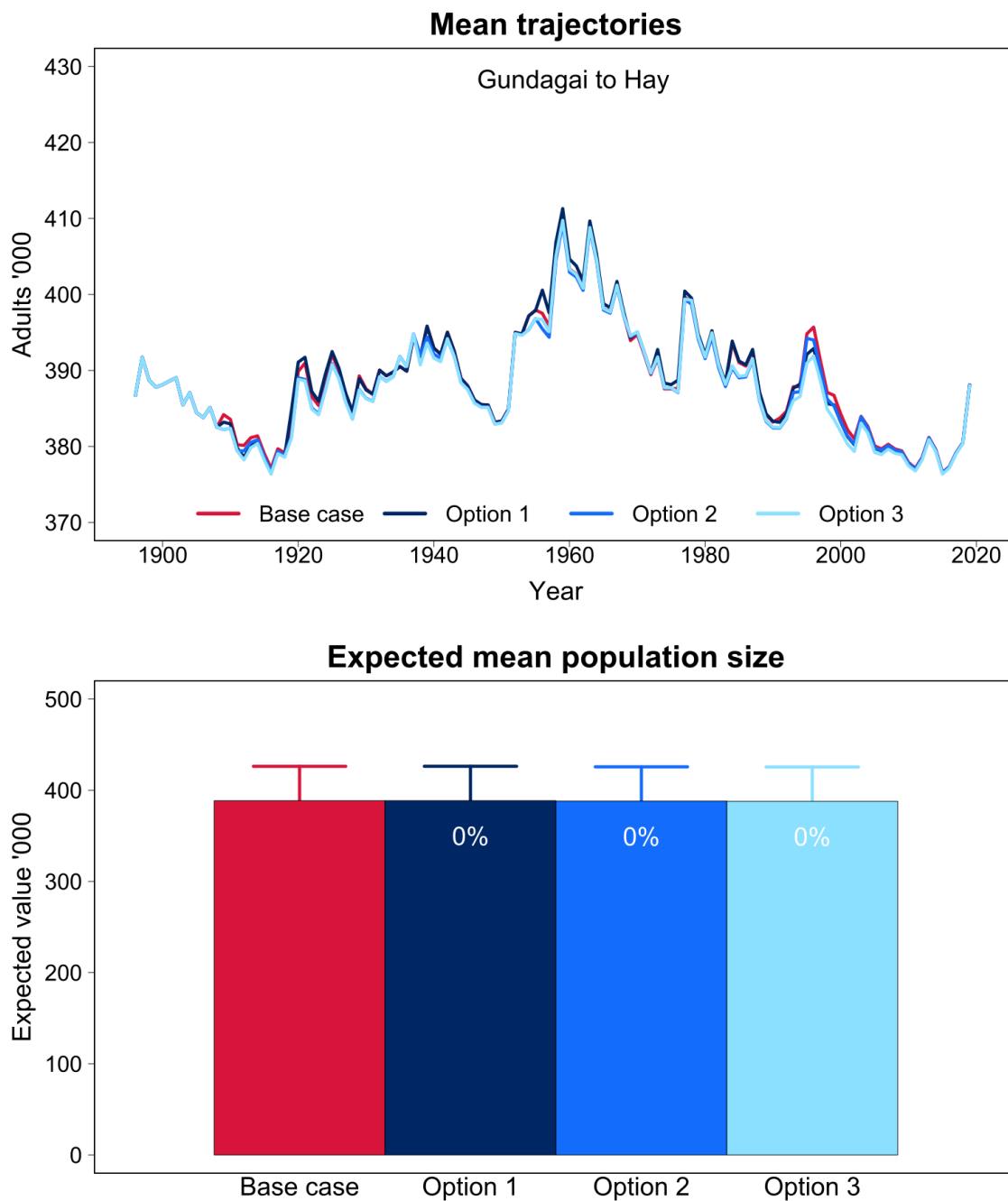


Figure 29. Modelled Carp adult population size in the Gundagai to Hay reach (Murrumbidgee River). Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar. There were very similar temporal trends in the adult population size among flow scenarios and no difference between the associated expected mead adult population sizes. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Hay to Balranald population

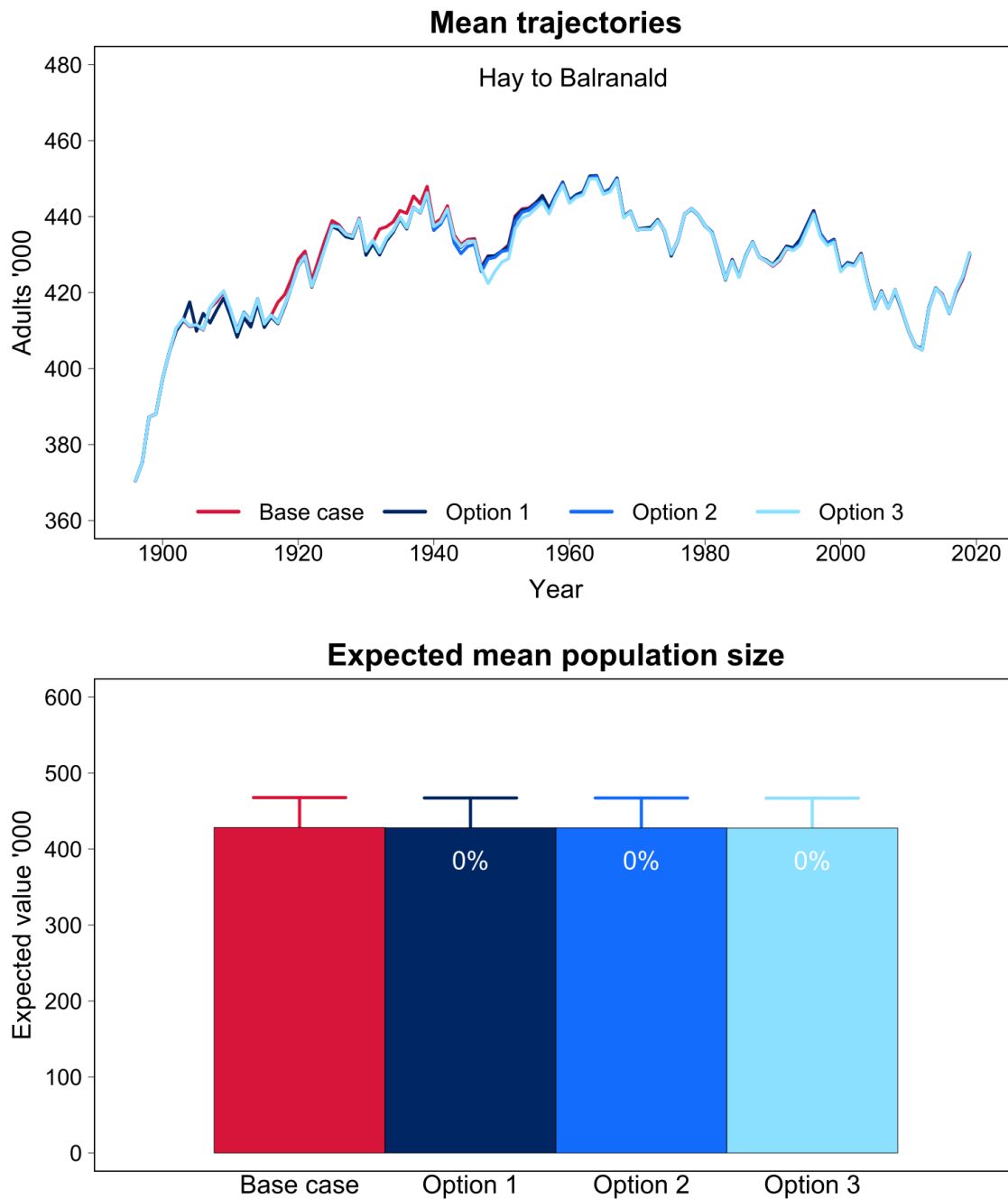


Figure 30. Modelled Carp adult population size in the Hay to Balranald reach (Murrumbidgee River). Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar. There were very similar temporal trends in the adult population size among flow scenarios and no difference between the associated expected mead adult population sizes. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Adult Carp mean population trajectories and expected mean population sizes for the hydrological years 1990–2019

Total populations

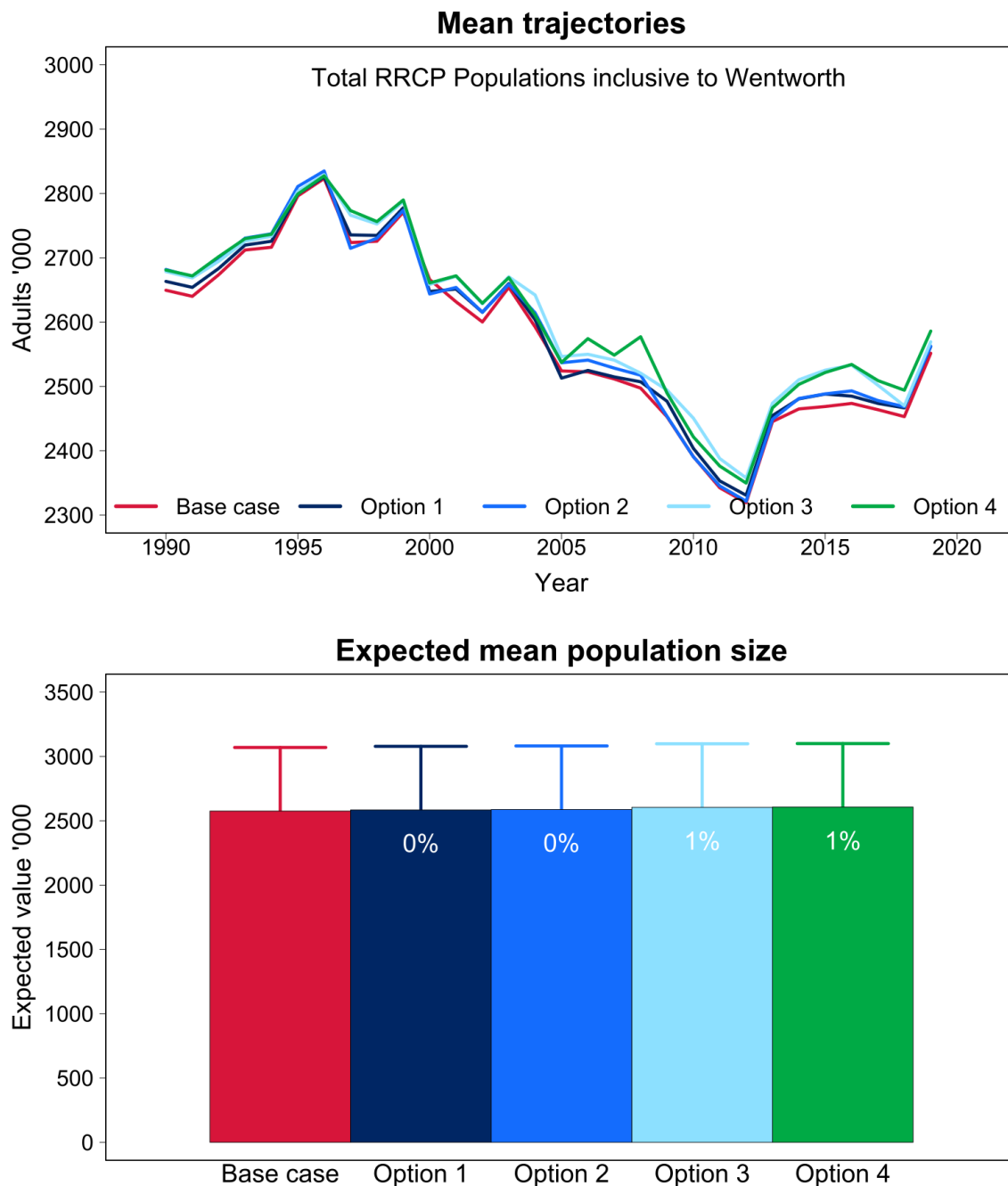


Figure 31. Modelled Carp adult population size across all modelled reaches in the southern Murray–Darling Basin for the hydrological years 1990–2019. Top panel: average adult population size, and Bottom panel: expected values of the mean population size relative to the Base case, with percentage change from the Base case shown in each bar. The total predicted adult Carp population declined from 1995 which encompassed the Millennium Drought. This period signified relatively low flows and low inundation of floodplain habitats across the studied reaches, which likely restricted Carp reproduction and recruitment. There was also a recovery in the population post the early 2010s period.

Early life-history responses of Carp

Total populations

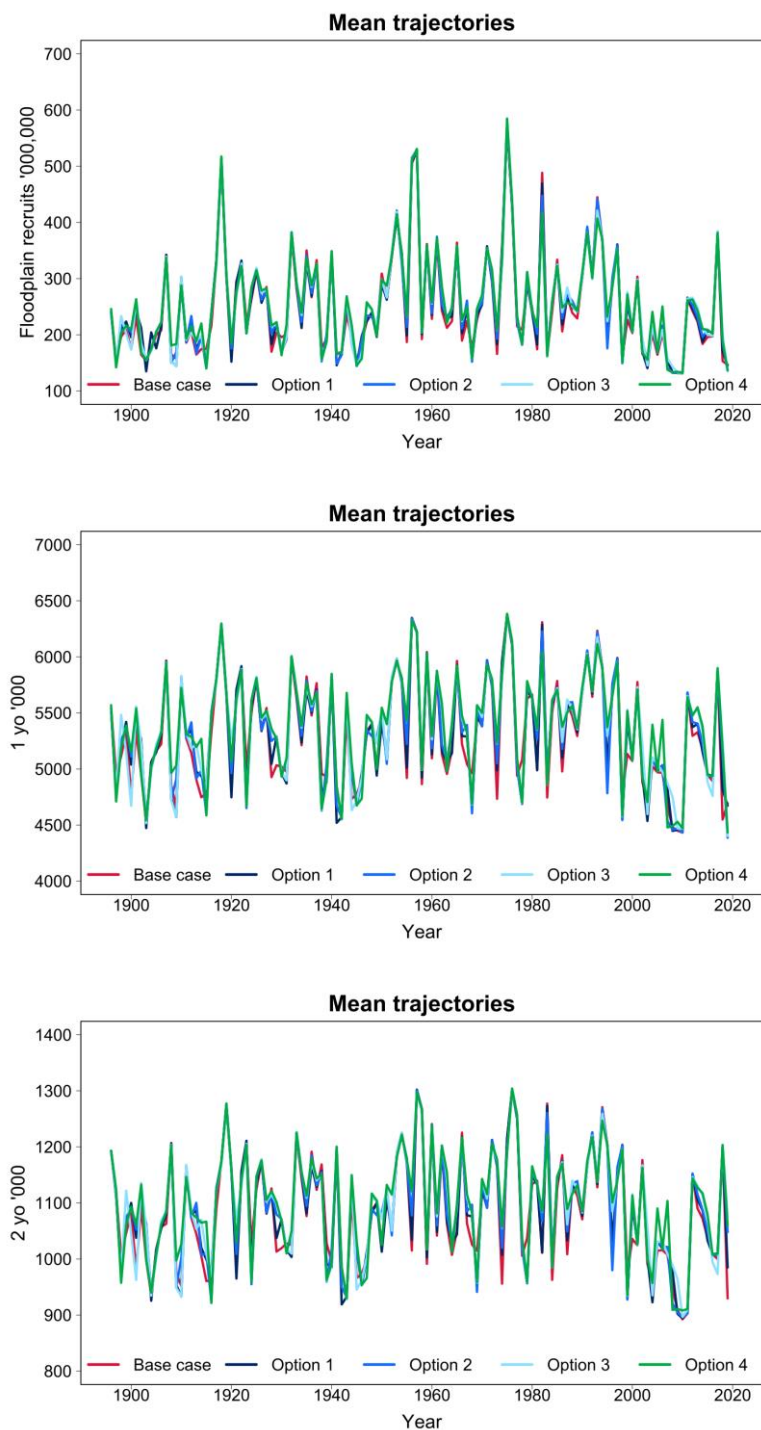


Figure 32. Predicted early life-history responses of Carp across all modelled program reaches in the southern Murray–Darling Basin. Lines show the Base case trajectories compared to flow scenarios 1–4. Top panel shows mean floodplain recruit (fingerlings) trajectories. Middle panel shows mean 1-year-old population trajectories and the bottom panel shows 2-year-old population trajectories. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

3.2 Interpreting hydrological inputs

As floodplain habitat (H10 habitat) is the strongest driver of Carp population responses and to help explain the results in Carp dynamics we plot the deviance of differing maximum yearly floodplain inundation under the of the highest flow limit scenarios considered in this project (Option 4 – Murray; and Option 3 – Murrumbidgee). Deviance is calculated as the proportional inundation of floodplain habitat (H10 habitat) of the highest flow limit option less the proportional inundation of the base case scenario through years. Each panel in Figure 33 represents deviance for the differing populations in this study and this plot shows that there is relatively little difference (on average) between the base case (current operations) and the highest flow limit level under consideration in this project.

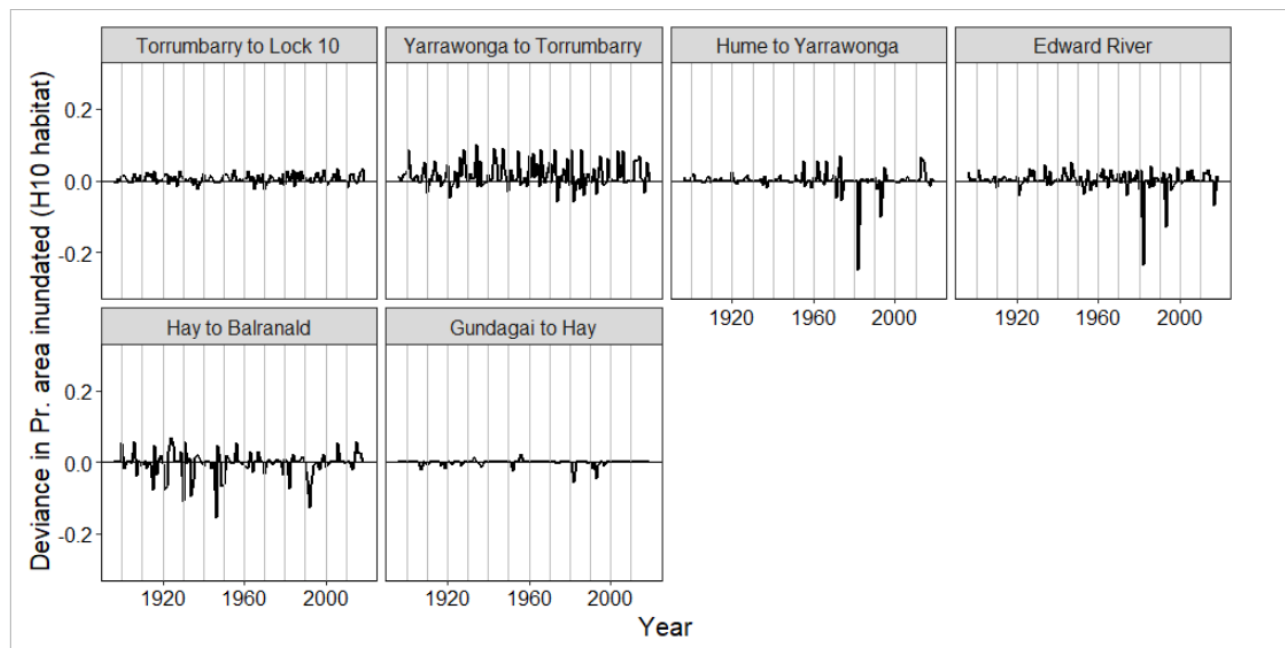


Figure 33. Deviance plot of differing maximum yearly floodplain inundation under flow scenarios considered in this project. Deviance is calculated as the proportional inundation of floodplain habitat (H10 habitat) of the highest flow limit option (Option 4) minus the proportional inundation of the Base case scenario through years. Each panel represents deviance for the differing populations in this study. Floodplain habitat (H10 habitat) is shown as it is the strongest driver of Carp population responses.

3.3 Sensitivity analysis

Conventional sensitivity analysis shows the model is most sensitive to estimates of juvenile survival (Figure 34), although elasticity analysis indicates that the strength of this sensitivity is less than 1 (Figure 34). The consequences of elasticity being less than 1 can be seen in **Error! Reference source not found.**, where a $\pm 10\%$ change in any juvenile survival rate only produces a -1.42% to 1.36% change in the underlying population growth rate, highlighting that the most sensitive component of the model, juvenile survival rates, produces only small changes in the population growth rate for relative large changes in the parameter. Only when all survival rates are modified by 10% is there a greater than 10% response in the population growth rate, pointing to the model being relatively insensitive to changes in input parameters. The reproductive value highlights that Carp contribute to future generations over a wide range of age classes (Figure 34).

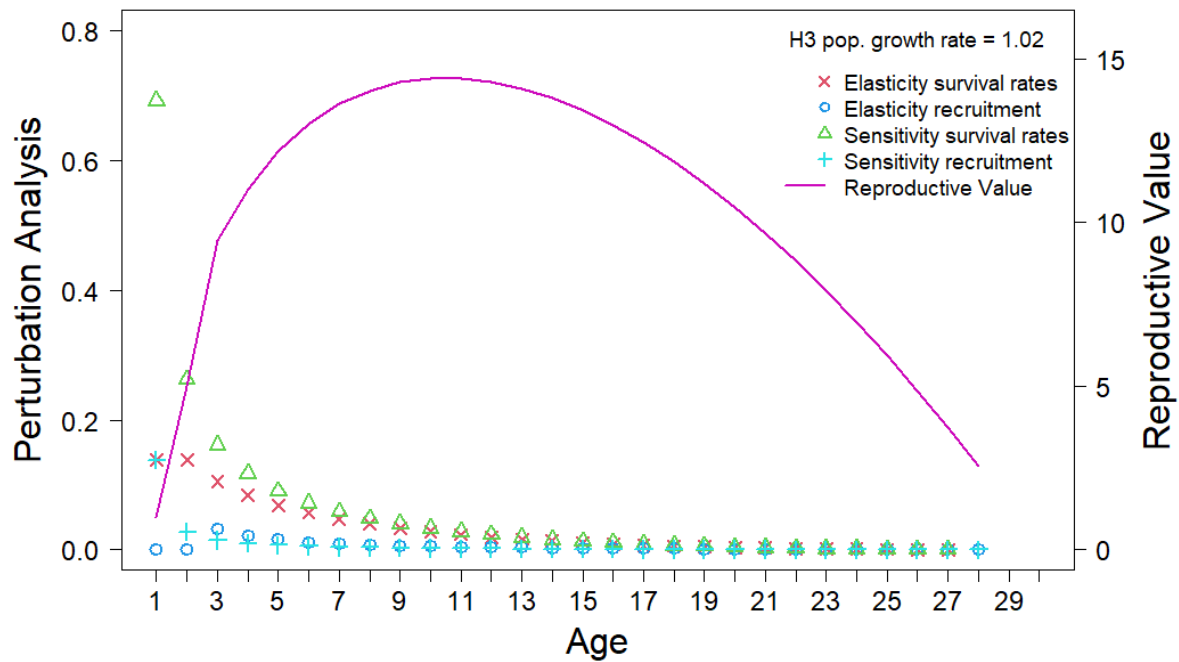


Figure 34. Analytic sensitivity analysis of the matrix model in Figure 20 parameterised with survival rates from Table 2 and H3 from Table 5.

Table 9: Sensitivity analysis of the matrix model in Figure 20, parameterised with survival rates from Table 2 and H3 from Table 5 as solutions to the characteristic polynomial $\det[\text{CarpModel} - \lambda I] = 0$ expressed as changes in the vital rates (parameter), the growth rate (λ) and percentage change in the growth rate from changes to the vital rates compared with H3: $\lambda = 1.0188$.

Parameter	-10%		+10%	
	λ	%change	λ	%change
$S_e - S_2$	1.0044	-1.42	1.0327	1.36
All adult S	0.9610	-5.67	1.0798	5.99
All $S_1 - S_{27}$	0.9307	-8.64	1.1063	8.59
All S	0.8803	-13.60	1.1690	14.74
All Fec	1.00445	-1.42	1.0327	1.36
All	0.8694	-14.66	1.1870	16.51

Doubling or halving the rate of floodplain access did not markedly alter predicted mean population sizes (Figure 35–Figure 38). While there were differences between the standard, DR and HR scenarios (depending on reach modelled), when comparing expected values of the mean population size for the base case with Option 4, the response was consistent across all scenarios (Figure 35–Figure 38). This indicates that the impacts of Option 4 (relative to the base case) are insensitive to underlying assumptions around floodplain access (Figure 35–Figure 38). Depending on the reach modelled, there were differences between scenarios. However, the DR scenario did not produce greatly increased numbers of adult Carp on average as the flows modelled did not

significantly increase Carp access to the floodplain in comparison to the base case (compare Figure 35 with Figure 38).

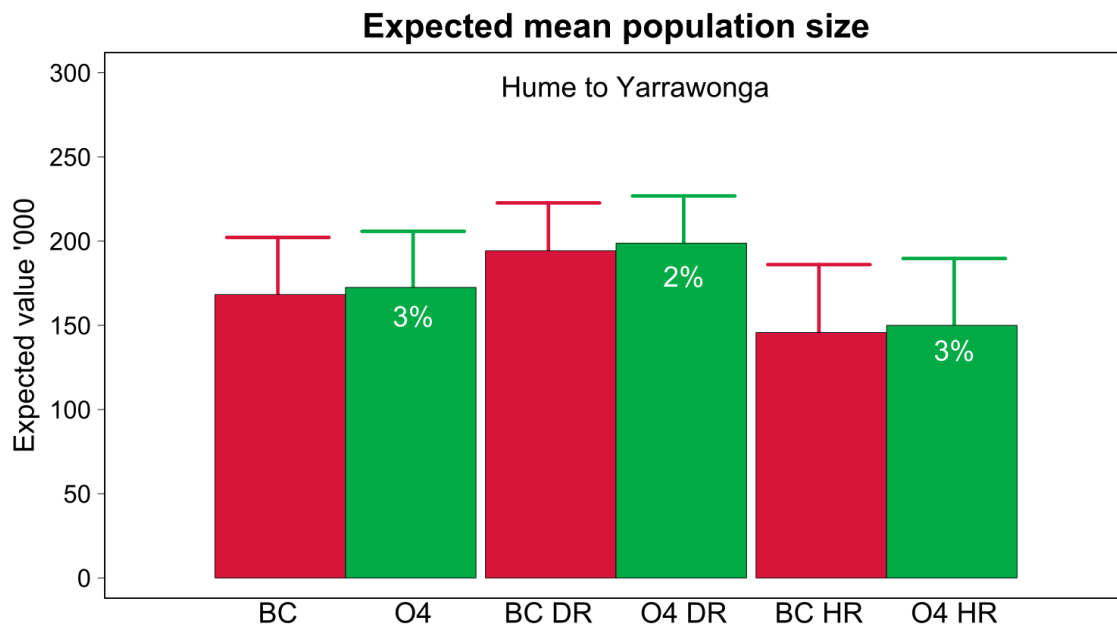


Figure 35. Hume to Yarrawonga expected values of the mean population size for the Base case (BC) and Option 4 (O4) for modelled Carp access to the floodplain, double rate of access to the floodplain (DR), and half rate of access to the floodplain (HR). Percentage change from the relevant Base case shown in each Option 4 bar.

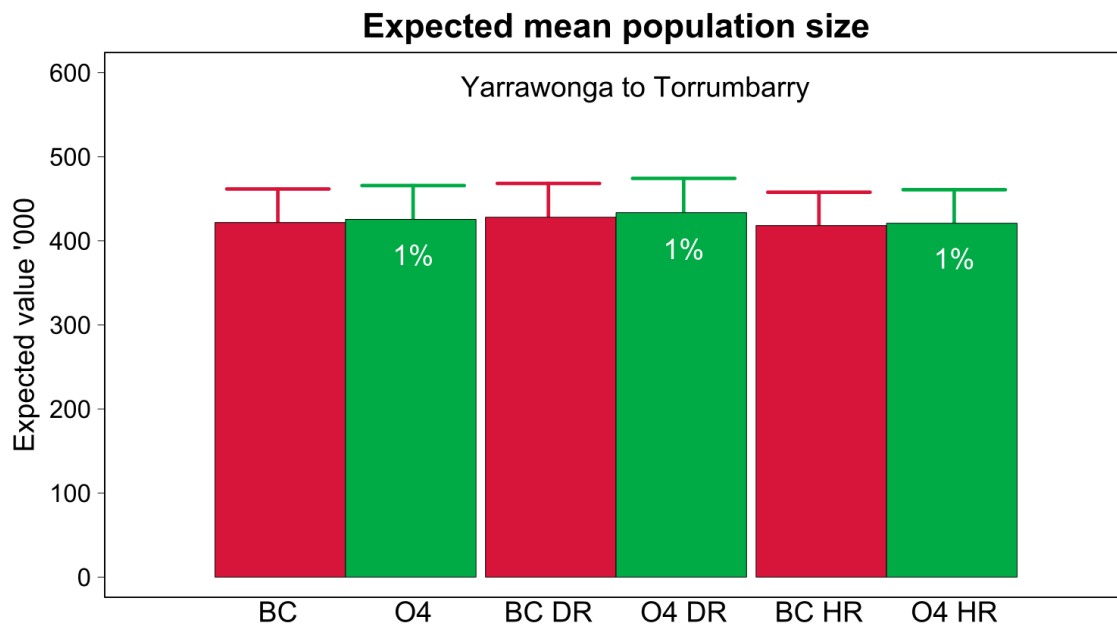


Figure 36. Yarrawonga to Torrumbarry expected values of the mean population size for the Base case (BC) and Option 4 (O4) for modelled Carp access to the floodplain, double rate of access to the floodplain (DR), and half rate of access to the floodplain (HR). Percentage change from the relevant Base case shown in each bar.

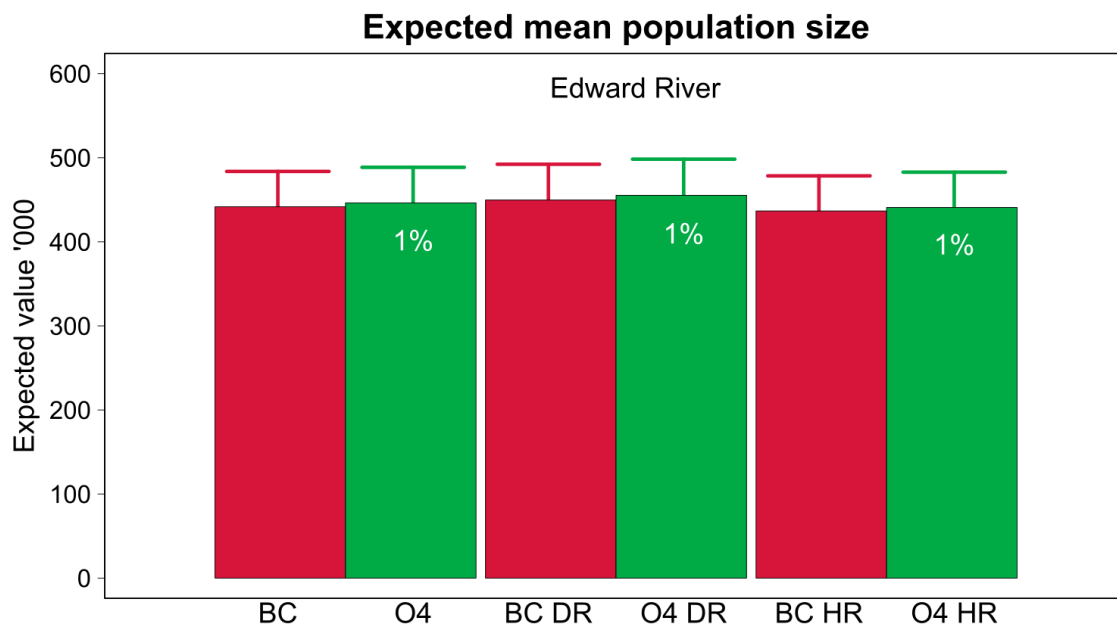


Figure 37. Edward River expected values of the mean population size for the Base case (BC) and Option 4 (O4) for modelled Carp access to the floodplain, double rate of access to the floodplain (DR), and half rate of access to the floodplain (HR). Percentage change from the relevant Base case shown in each bar.

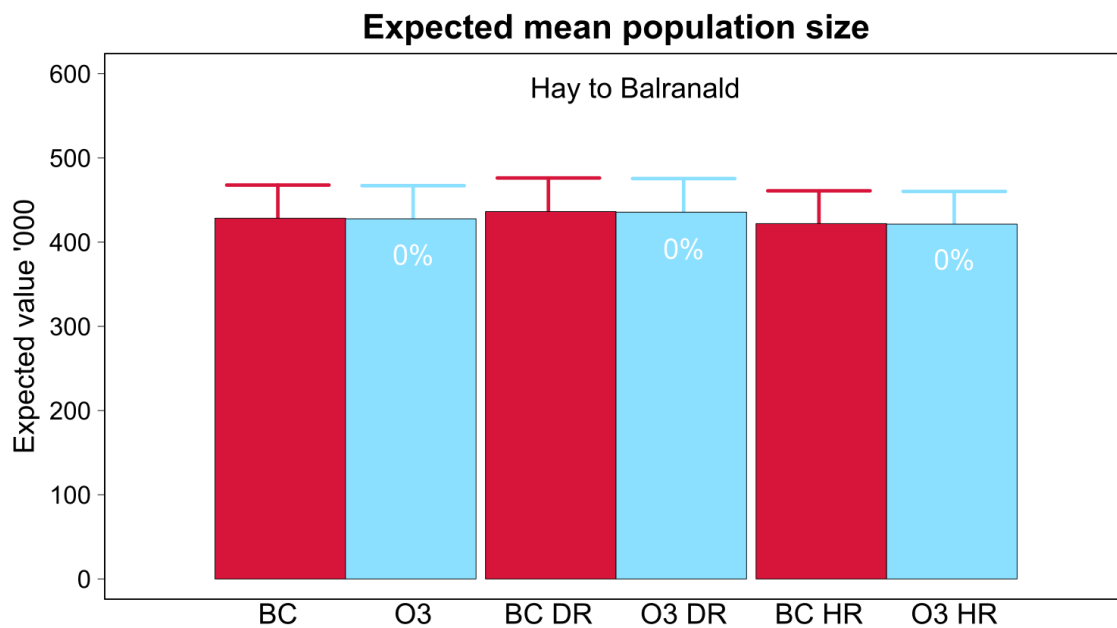


Figure 38. Hay to Balranald expected values of the mean population size for the Base case (BC) and Option 4 (O4) for modelled Carp access to the floodplain, double rate of access to the floodplain (DR), and half rate of access to the floodplain (HR). Percentage change from the relevant Base case shown in each bar.

4 Discussion

4.1 Key findings

Carp populations are broadly stable over time with key fluctuations driven by major climatic drivers

The Carp model used >120 years of modelled hydrological data (1896–2019) to predict the effects of proposed changes to environmental flows under the program on Carp population dynamics. Modelling over this extended period allowed exploration of carp population outcomes under a range of historical climate conditions. Here, the predicted Carp populations were broadly stable through time (i.e. there were no significant declines or increases above or below the starting population sizes), but had short periods of predicted population decline and increase. For example, there were several periods of population decline (e.g. hydrological period represented by the late 1930s and 1940s—contemporary with the WWII Drought) and increase (e.g. hydrological periods after 1919 and in the 1950s). These periods were generally consistent across the modelled populations and coincided with periods of low and high river flows, respectively (see Appendix 4 for plots of inundated habitat area through time for each modelled population area). When model observations were extracted for the most recent 30-year period (1990–2019), the predicted adult population size (summed across populations in each year) decreased significantly (~20% decrease), likely as a response to the Millennium Drought and associated lower flows and floodplain habitat inundation.

These modelled results broadly align with empirical observations from electrofishing surveys in the southern MDB (Figure 39): uncorrected total Carp count data, collated by Koehn et al. 2016 (see Figure A3.2 in Koehn et al. 2016), plotted with total Carp output (juveniles and adults) from the population models. Both modelled output and count data were normalised by transforming to a standardised z-score to allow comparisons between the two different data sets, and the trajectory of best fit was plotted as an example trajectory from model output approximating the count data (Figure 39). Generally, the normalised modelled output declines in the late 2000s and recovers post 2010, however the trajectory of best fit in both base case and Option 4 outcomes declines earlier, and not as sharply as most trajectories and in line with the normalised total Carp count data, identifying that the model produces trajectories similar in pattern to the count data. Furthermore, the normalised total Carp count data falls within the range of normalised outcomes from the population model. We note, however, that empirical estimates of abundance generated without contextualisation of survey efficiency (i.e. electrofishing efficiency) should be interpreted with caution (Lyon et al. 2014, Todd et al. 2022).

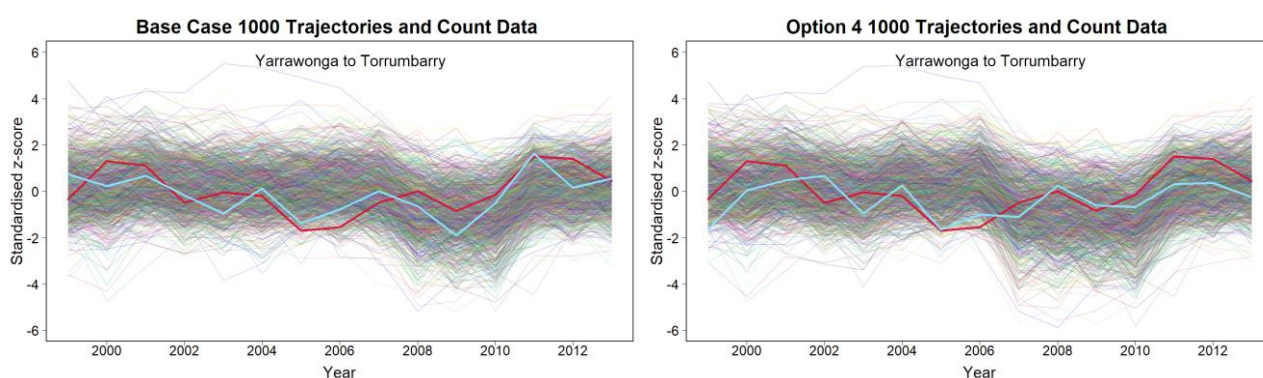


Figure 39. Total Carp Base Case trajectories, total Carp count data (red line) and best fit trajectory (blue line) in the left panel and total Carp Option 4 trajectories, total Carp count data (red line) and best fit trajectory (blue line) in the right panel. The best fit lines identify that model output plausibly matches the dynamics of the normalised total Carp count data and that the normalised total Carp count data falls within the range of normalised outcomes produced by the population model.

Our predictions also broadly align with an independent study recently developed a Bayesian network approach to model Carp population abundances in the MDB as a function of environmental predictors (e.g. water temperature, velocity and inundation state) (Graham et al. 2021). Unlike our population modelling approach,

Bayesian networks do not explicitly model population dynamics (i.e., inter-annual links between births, deaths and movement), nor does their approach include explicit comparisons of hydrological scenarios. Despite these differences, the Graham et al. (2021) study and our study predict similar patterns in carp abundances through time and in response to broad hydrological patterns in the mid-Murray River region. Specifically, both approaches predict declines in recruitment and adult populations during the Millennium Drought, and subsequent recovery in the period after the year 2010.

Individual Murray River Carp populations generally reflected the dynamics of the total (aggregated) population, except in the Hume to Yarrawonga reach. In the Hume to Yarrawonga reach, the population generally declined in all periods, except when there were large floods, in which case the adult population observed large increases. This response was driven in this instance by the relatively low levels of floodplain habitat inundation in average flow years, interspersed with large floodplain inundation during floods. We note that the magnitude of decline in Murrumbidgee River populations during the Millennium Drought (in particular in the Hay to Balranald reach) was not as large as the magnitude of decline modelled in the Murray River populations, with generally more stable predicted adult populations, likely due to the relatively consistent inundations of the lowland floodplain habitats along these reaches. Empirical observations of Carp in the Murrumbidgee River suggest a similar pattern to the Murray system with population increases associated with widespread flooding and population declines during the Millennium Drought (Gilligan 2005). The cause of the difference in decline magnitude warrants further investigation, and, in the case of the Hay to Balranald population, it may relate to differing behaviour (e.g. habitat use) or early life-history responses to habitat inundation (e.g. survival rates) of Carp in this reach.

The broad predictions of Carp population responses were driven by wide-ranging southern MDB hydrological patterns, which can be seen in the analysis of floodplain inundation model inputs (Figure 21 **Error! Reference source not found.** and Figures A4.39 - A4.44), where, for example, floodplain habitats were inundated relatively little during the Millennium Drought. Other periods (e.g. after 1919) saw large floodplain habitat inundation driven by natural flooding events, which resulted in higher predicted recruitment and adult population sizes. We note the difference between these broad hydrological periods and the relatively small increases in floodplain habitat inundation predicted to occur under flow scenarios (i.e. compare the extent of floodplain inundation caused by natural floods relative to the increase caused by flow scenarios in Appendix 4; further discussed below) As such, the population modelling approach taken here is demonstrated to be sensitive to hydrological inputs (i.e. inundation of Carp habitats through time).

Overall there was negligible change to carp populations under flow scenarios

When the flow scenarios are considered, the Carp population modelling predicted very little difference among the different flow scenarios (i.e. Options 1–4) relative to the base case (i.e. 15,000 ML day⁻¹ at Yarrawonga and 25,000 ML day⁻¹ at Doctors Point in the Murray River, and 22,000 ML day⁻¹ at Wagga Wagga in the Murrumbidgee River). When predicted Carp responses were amalgamated across all modelled program populations, flow limit Option 1 predicted mean adult population sizes equal to the Base case scenario, and flow scenarios 2–4 predicted adult population sizes 1% above the Base case. If individual populations are considered, the highest flow limit option increased predicted adult Carp populations marginally in some populations (e.g. a 3% higher adult population size under Option 4 relative to the Base case scenario in the Torrumbarry to Wentworth and Hume to Yarrawonga reach populations), with no differences between flow scenarios in either of the Murrumbidgee populations.

If instead of adult responses we examine predicted juvenile Carp responses, there were relatively little difference between flow scenarios and the Base case scenario, although there were large recruitment spikes across hydrological scenarios during wet periods.

Quantitative modelling predicted relatively little change in the adult Carp population under any of the flow scenarios considered in this study (relative to the Base case). However, adult Carp impact on aquatic values (e.g. water quality and aquatic plants) at reasonably low densities (e.g. 80–100 kg ha⁻¹, Brown and Gilligan (2014); with some aquatic values impacted at < 50 kg ha⁻¹, Vilizzi et al. 2015). We speculate that Carp populations are already above these density-impact thresholds for much of their southern MDB range (Stuart et al. 2021b), and hence, require an integrated program of management to reduce impacts. Given public concern related to already severely degraded native fish populations (Koehn and Lintermans 2012; MDBC 2004), optimising flow regimes to promote native fish is of paramount importance (Todd et al. 2022). Hence,

decisions that have significant benefits for native fish are, on balance, desirable even where there can be parallel benefits to Carp (Forsyth et al. 2013). The use of population models enables managers to make these choices in full knowledge of potential conflicts between native fish and Carp in their responses to water management actions.

4.2 Drivers of carp population responses under flow scenarios

Relatively small changes to inundation regimes under flow scenarios

The relatively small increases in predicted adult Carp populations under the program increased flow limit scenarios are expected based on the modelled drivers of Carp population dynamics. Increased flow limits under the program are expected to increase the frequency of wetland and low-level floodplain connecting flows by only relatively small amounts (i.e. 5–15% (DPE 2022)), and this is reflected in the estimates of habitat inundation derived from the RiM-FIM and EW-FIM models (Overton et al. 2006, Sims et al. 2014 and see Appendix 4). Here, the hydrological difference between base case and Option 4 estimates of yearly maximum floodplain inundation were relatively small (i.e. usually < 5%; see Figure 21 and Appendix 4). Again, these small differences are to be expected as the targeted flow releases under flow scenarios span only 5 days in the Murrumbidgee River and less than 25 days (14 or 21 days) in the Murray River. Consequently, the contribution of program flows to the 25-day maximum habitat inundation model inputs (chosen as they represent the Carp reproductive cycle) will be reduced. Additionally, the scale of wetland inundation increases under flow scenarios are small when compared to large unregulated events (DPE 2022).

Furthermore, extent of inundation during large unregulated events was sometimes larger in the base case scenario than in the higher flow scenarios (see Figure 33). These instances of higher inundation under the base case scenario may be due to differences in (modelled) storage volumes and natural spill events through time across the differing scenarios (i.e. differences in modelled e-water delivery between flow scenarios creating differing air-space within dams, which influences subsequent dam spillage, (DPE, 2022)). However, the implications of program deliveries for storage dynamics is under further investigation. These hydrological inputs and floodplain inundation estimates form a key driver of Carp population dynamics within the population model and, as such, explain the small difference of predicted adult Carp populations among hydrological scenarios.

Short-term increases to carp populations in periods when environmental flows make up a significant proportion of higher river flows

When focusing on fine-scale predicted Carp recruitment patterns (i.e. individual years) rather than the broad-scale patterns (i.e. decades and centuries) as discussed above, the models reveal some small, predicted increases in Carp populations under increased flows from program scenarios; specifically in terms of higher predicted Carp recruitment and adult population sizes. This can be seen across all modelled populations, with predicted adult population sizes sometimes ca. 50,000 larger under the highest flow scenario compared with under the base case during short periods of time (e.g. 1910s and 2010s). These predicted population increases often occurred after periods of population decline and in conjunction with a significant increase in floodplain habitat inundation extent under increased flow scenarios, when environmental flows made up a significant proportion of total river flows. Hence, program scenarios did increase predicted Carp population sizes during some shorter time periods. Nevertheless, increases in floodplain habitat inundation were not prevalent enough to drive a strong predicted Carp population increase over the long-term extent of this study. This finding supports our focus on long-term predicted Carp population trends rather than short-term effects.

Competition over resources mean short-term juvenile population increases do not translate to increased numbers of adult Carp over the long term

Another mechanism that potentially reduced the impact of increased flows under the program scenarios was the density-dependence construct within the model. Density dependence was applied to juveniles at the point of migration from the floodplain to the river when juveniles transition from pelagic to a predominantly benthic feeding, and thus, enter into direct competition with older Carp. The underlying importance of the density-dependence construct is that it acts to dampen floodplain recruitment spikes by increasing mortality at the 0+ to 1-year-old life-stage transition where high mortality is usually experienced (Brown et al. 2005). This density-

dependence mechanism is further supported by empirical data, where recruitment events (i.e. large cohorts of juvenile Carp) commonly do not transition fully into the adult Carp population in subsequent years (Stuart and Jones 2006b; Koehn et al. 2018; Fredberg et al. 2019). These empirical observations support our inclusion of a density-dependence mechanism within the population model. Although this density-dependence mechanism may have dampened large Carp recruitment events, thus dampening differences among program hydrological scenarios, similarities between predicted responses to flow scenarios were most likely due to the small differences in inundation extent among flow scenarios. The full extent to which the density-dependence mechanism represents natural phenomena is difficult to ascertain, due to the difficulty associated with testing these mechanisms (i.e. it is difficult to collect data on density dependence: Todd et al. 2004), but this should be further explored in the future.

4.3 Model sensitivity to Carp movement rates and population responses to differing habitats

Model sensitivity to assumptions about the attractiveness of the inundated floodplain habitats to Carp was assessed with changes to the underlying assumption of Carp movement onto the floodplain. Specifically, we considered two alternative levels of movement: 1) doubled rate (DR) of movement on to the floodplain; and 2) halved rate (HR) of movement on to floodplain. We found little change between Option 4 and the base case irrespective of the rate of floodplain access. Depending on the reach modelled, there were differences between scenarios. However, the DR scenario did not translate into greatly increased numbers of adult Carp on average, most likely because the flows modelled do not significantly increase Carp access to the floodplain in comparison to the Base. We conclude that the model is largely insensitive to the assumed rate of access to the floodplain and, therefore, this assumption has minimal influence on the predicted impacts of the flow limit options considered in this report.

Additional sensitivity analysis was undertaken for a range of estimated early life history stage (ELHS) survival rates encompassing the different aquatic habitat types (Table A2.1 and Table A3.1). The various configurations of different ELHS survival rates in Table A3.1 allow for a ranging sensitivity analysis of the effects of ELHS variation population dynamics. Without exception, the model is most sensitive to changes in 1-year-old survival rates, regardless of ELHS configuration, though the strength depends on the ELHS configuration, with increasing sensitivity associated with higher population growth rates. This result highlights that while the model has minor sensitivity to estimates of ELHS survival, there is nothing unexpected in this outcome (c.f. Todd et al. 2004; 2017a; b; 2018; Stossel et al 2022). Moreover, while the model is sensitive to changes in ELHS survival, although these differences are not affected by the flow scenarios, the absolute abundances will change, but not the relative differences among the flow scenarios.

4.4 Comparisons with native fish responses to considered flow scenarios

The predicted responses of Carp to flow scenarios are in contrast with similar modelling performed for native fish species (Murray Cod and Golden Perch; Todd et al. 2022). The responses to program flow limit scenarios were relatively minor for Murray cod (i.e. there was little effect of increased flow limits on the population), but were much larger for Golden perch (i.e. there were incremental benefits as flow limits increased up to a maximum of 30% predicted increase for program flow limit Option 4). For Carp, access to floodplain habitats has been identified as important for breeding (Koehn et al. 2016), and the model construct is based on habitat inundation as a key driver of spawning and recruitment success. This contrasts with the ecology and subsequent model architecture of Golden perch and Murray Cod, where riverine flow pulses trigger large-scale movement in the former species (O'Connor et al. 2005, Koehn and Nicol 2016, Zampatti et al. 2019) and spawning in the latter species depends on rising temperature and lotic conditions (Lake 1967, Koehn and Harrington 2006, Stuart and Sharpe 2021). Consequently, the differing hydrological inputs and model constructs (based upon the specialised biology and ecology of each species) of the three species underscore the differences between predicted responses to program flow limit scenarios. For example, the Golden Perch model construct is designed as a metapopulation model, where flow pulses trigger spawning events and large-scale movements between each population (larval drift, juvenile and adult movement are included). Murray Cod spawning and recruitment are estimated via an empirically derived flow and temperature model, with flow-temperature relationships specific to each reach (Todd et al. 2022). As the program flow limit

options are designed to facilitate connectivity between habitats rather than the delivery of large floods or lotic conditions (DPE 2022), the larger predicted benefits to Golden Perch relative to Murray Cod and Carp are expected outcomes.

4.5 Future steps

The Carp population model has not undergone a formal validation process, which would increase confidence in predicted model outcomes and identify critical knowledge gaps to be targeted with empirical data collection. Formal validation would include a comparison of model predictions (e.g. population size) with empirical observations from independent datasets (see Todd et al. 2022). Validation can be used to identify specific conditions (e.g. high or low flows) and processes (e.g. spawning or adult survival) for which the model generates reliable or unreliable predictions, thus informing updates to the rules that underpin the model.

Modelling additional flow scenarios, such as including a range of future climate change scenarios (i.e. with protracted periods of low/regulated flows with little floodplain inundation and protracted wet periods with frequent major floods), would provide crucial management insights. For example, modelling a protracted wet period scenario would allow for the examination of model behaviour at the upper limits of the Carp populations, which would in turn provide further context for evaluating management-focussed scenarios and the density-dependence mechanism. Conversely, modelling a 'climate change scenario' would involve the use of plausible future predicted flows to drive model predictions (as opposed to backwards projections of flows under current water management as used here), where for example changes in environmental water availability or use could impact upon Carp responses to flow limit options. We did include several sensitivity analyses on key model assumptions in this project (habitat attractiveness, habitat associated survival rates), but future sensitivity analyses on other model assumptions (e.g. modified sex ratios) would also be beneficial. Finally, including Carp populations in additional locations (e.g. the lower Darling River, the lower Murray River, major wetlands/tributaries and specifically Carp 'hotspots') would enable the construction of a metapopulation model, which would provide insight into Carp responses to management actions at a whole-of-basin scale.

In summary, potential future work includes:

1. Consider formal validation to increase confidence in the Carp population model predictions noting that suitable empirical abundance records may be required in order to do this.
2. Consider Carp population modelling for additional flow scenarios to provide further management knowledge, including a major flood scenario (e.g. 100,000 ML day⁻¹ at Yarrawonga and Wagga Wagga), and a future climate change scenario.
3. Consider additional population locations (e.g. the lower Darling River, the lower Murray River, major wetlands and tributaries) and the construction of a metapopulation model to enable greater insight into Carp population dynamics and potential control options.³⁰

4.6 Conclusions

The program flow limit options appear to have minimal impact on Carp populations compared to base case flow conditions. This suggests that the flow scenarios considered in the program can be tailored to maximise benefits to native flora and fauna with relatively little contribution to the invasive Carp population. Model sensitivity analyses show the findings are robust under adjustments to a number of model parameters and assumptions. The broad alignment of predicted adult carp populations with empirical observations from electrofishing surveys and other modelling approaches provide further confidence in the model and findings. We note that the Carp population model has not been formally validated, as has occurred for the models of native fish in the program. Confidence in the Carp model predictions would be improved by such a validation. We note that empirical estimates of Carp population abundance are scarce in the literature, and recommend targeted research in this area. Nonetheless, the population modelling approach represents a highly valuable tool to predict future responses to hypothetical hydrological regimes at a population processes level. For river managers, the flow scenarios do not appear to exacerbate an already serious situation, where Carp are well beyond density-impact thresholds in much of the southern MDB (Stuart et al. 2021b).

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6 Appendices

6.1 Appendix 1. Project team

Key ARI personnel and their roles in this project were:

- Dr Henry Wootton, Scientist and population modeller.
- Dr Charles Todd, Senior Scientist and population modeller.
- Dr John Koehn, Senior Scientist and ecologist.
- Dr Ivor Stuart, Program Leader and contact officer.

Additional scientific support was provided by other ARI staff, including Dr Scott Raymond, Dr Jarod Lyon, Dr Rob Hale, and Dr Ben Fanson. The project was supported by a range of other BCS staff and appointed experts, especially Dr Jason Thiem (NSW DPI Fisheries), and Dr Clayton Sharpe (NSW Parks and Wildlife Service).

6.2 Appendix 2. Description of habitat types used for Carp scenario modelling

Table A2.1. Description of habitat types used for Carp scenario modelling (from Koehn et al. 2016). The present modelling utilised habitats #3, #6 #8, #9 and #10.

No.	Habitat type	Description
H1	Main channel (mid upper Murray)—base flow	Low level not topped up by irrigation flows <50% bankfull. Only occurs during severe drought
H2	Main channel (mid upper Murray)—cover benches	50–70% bankfull irrigation flow
H3	Main channel (mid upper Murray)—bankfull	70% to bankfull irrigation flow
H4	Main channel (lower Murray)—base flow	Weir pools at operating height, low flows
H5	Main channel (lower Murray)—cover benches	Increase weir pool extent/influence (entitlement + irrigation flows + weir pools)
H6	River wetland, e.g. Barmah-Millewa Forest	Adjacent low-lying wetlands (without broader floodplain inundation)
H7	Wetland perennial, e.g. Kow Swamp	E.g. Barren Box Swamp. Off-stream wetlands with permanent water
H8	Wetland ephemeral, e.g. Hattah Lakes	Off-stream wetlands, high elevation wetlands that dry out if not reconnected
H9	Wetland permanently connected, e.g. adjacent weir pool	Wetlands now inundated permanently because of the weir pools follow weir pool dynamics, e.g. all unregulated weir pool wetlands in the lower Murray
H10	Natural floodplain inundation	Broad floodplain inundation (as per high-level natural floods)
H11	Artificial floodplain inundation, e.g. Chowilla	Inundated by regulators
H12	Lakes (off-stream), e.g. Lake Victoria	Lakes Victoria, Cargelligo; permanent water bodies
H13	Lakes (terminal), e.g. Alexandrina	Permanent water bodies at the end of the system
H14	Irrigation channels	High flow in irrigation season, then mostly dry/residual pools

6.3 Appendix 3. Survival rates for Carp in differing habitat types used in modelling

Table A3.1. Percentage survival elicited from expert opinion and the associated growth rate for each habitat type (from Koehn et al. 2016).

Habitat	Egg survival (%)	Larval survival (%)	Fingerling survival (%)	Young-of-the-year survival (%)	Population growth rate	Population doubling time
H1	0.72	1.82	3.31	6.31	0.77	–
H2	1.36	3.84	5.88	7.25	0.88	–
H3	2.45	5.24	6.89	11.00	1.02	35.00
H4	1.50	2.83	5.25	8.15	0.86	–
H5	2.69	5.24	7.36	12.01	1.06	11.90
H6	12.07	10.00	21.41	15.50	2.43	0.78
H7	4.68	7.10	14.84	14.76	1.52	1.66
H8	7.96	5.70	16.83	7.96	1.46	1.83
H9	6.45	6.54	14.84	21.12	1.78	1.20
H10	10.90	8.15	20.31	21.39	2.41	0.79
H11	12.19	11.65	13.51	26.31	2.60	0.73
H12	5.21	5.91	13.09	13.69	1.42	1.98
H13	6.37	7.52	15.03	17.05	1.74	1.25
H14	0.71	2.20	6.70	5.65	0.80	–

6.4 Appendix 4. Supplementary results

Supplementary outputs from the modelling scenarios have been provided here. Total adult population abundance was calculated and compared in relation to the Base case for the five flow scenarios. Expected adult minimum and maximum population sizes through time across flow limit scenarios have been presented here. Results for the summed responses across all modelled populations have been presented in Figure A4.1 and all modelled reaches in the Murray River (Figure A4.2; including the Edward River: Figure A4.7) and Murrumbidgee River (Figure A4.3). Individual reach outputs have also been presented for the Murray River from Hume to Yarrawonga (Figure A4.4), Murray River from Yarrawonga to Torrumbarry (Figure A4.5), Murray River from Torrumbarry to Wentworth (Figure A4.6), Edward River (Figure A4.7), Murrumbidgee River from Gundagai to Hay (Figure A4.8), and Murrumbidgee River from Hay to Balranald (Figure A4.9). Adult Carp expected minimum and maximum population sizes have been given for the years 1990–2019 in Figure A4.10. Outputs for predicted early life-history responses of Carp (mean population trajectories) have also been summarised across all modelled reaches and the Murray and Murrumbidgee River systems (Figure A4.11–Figure A4.13) as well as presented for individual reaches individually (Figure A4.14–Figure A4.19). Carp expected minimum and maximum population sizes for the early life history stage have been given for the years 1990–2019 in Figure A4.20. Finally, sensitivity to assumptions about attractiveness of inundated floodplain habitats to Carp have been shown in Figure A4.21–Figure A4.24 and conventional sensitivity analysis shown in Figure A4.25–Figure A4.38 for all habitat types in Table A2.1 and Table A3.1.

Predictions of adult Carp responses in terms of expected minimum and maximum population sizes were very similar to the mean population size (presented in the body of the report). Expected minimum population sizes were also very similar across flow scenarios in all modelled populations (Figure A4.1–Figure A4.9). When the temporal extent of modelling was confined to the 30-year period encompassing the hydrological years 1990–2019, the expected minimum and maximum Carp population sizes also reflected the expected mean population size (see Results) for the total population (Figure A4.10).

Juvenile predicted responses largely reflected those of adults, where again there was very little difference between flow scenarios across all study populations (Figure 32; Figure A4.11) or indeed among individual rivers or reaches (Figure A4.14–Figure A4.19, Figure A4.12, Figure A4.13, A4.18). Again, there was almost no difference in predicted juvenile responses to flow scenarios in the Murrumbidgee River at the river (Figure A4.13) or reach scale (Figure A4.18 and Figure A4.19). Juvenile predicted responses during the hydrological years 1990–2019 were similar across flow limit option scenarios, but all scenarios showed broad responses to hydrological inputs with a decline in recruitment (and subsequently 1- and 2-year-olds) during the Millennium Drought years and subsequent recovery in the following period (Figure A4.20).

Sensitivity to assumptions about attractiveness of inundated floodplain habitats to Carp shows some sensitivity to floodplain attractiveness, the relative differences among the flow scenarios are not sensitive to floodplain attractiveness (Figure A4.21–Figure A4.24). For sensitivity analysis of all habitat types see section: *Sensitivity analysis of the different habitat types available as a means of exploring sensitivity to alternative configurations of early life-history survival*.

Adult Carp expected minimum and maximum population sizes

Total populations

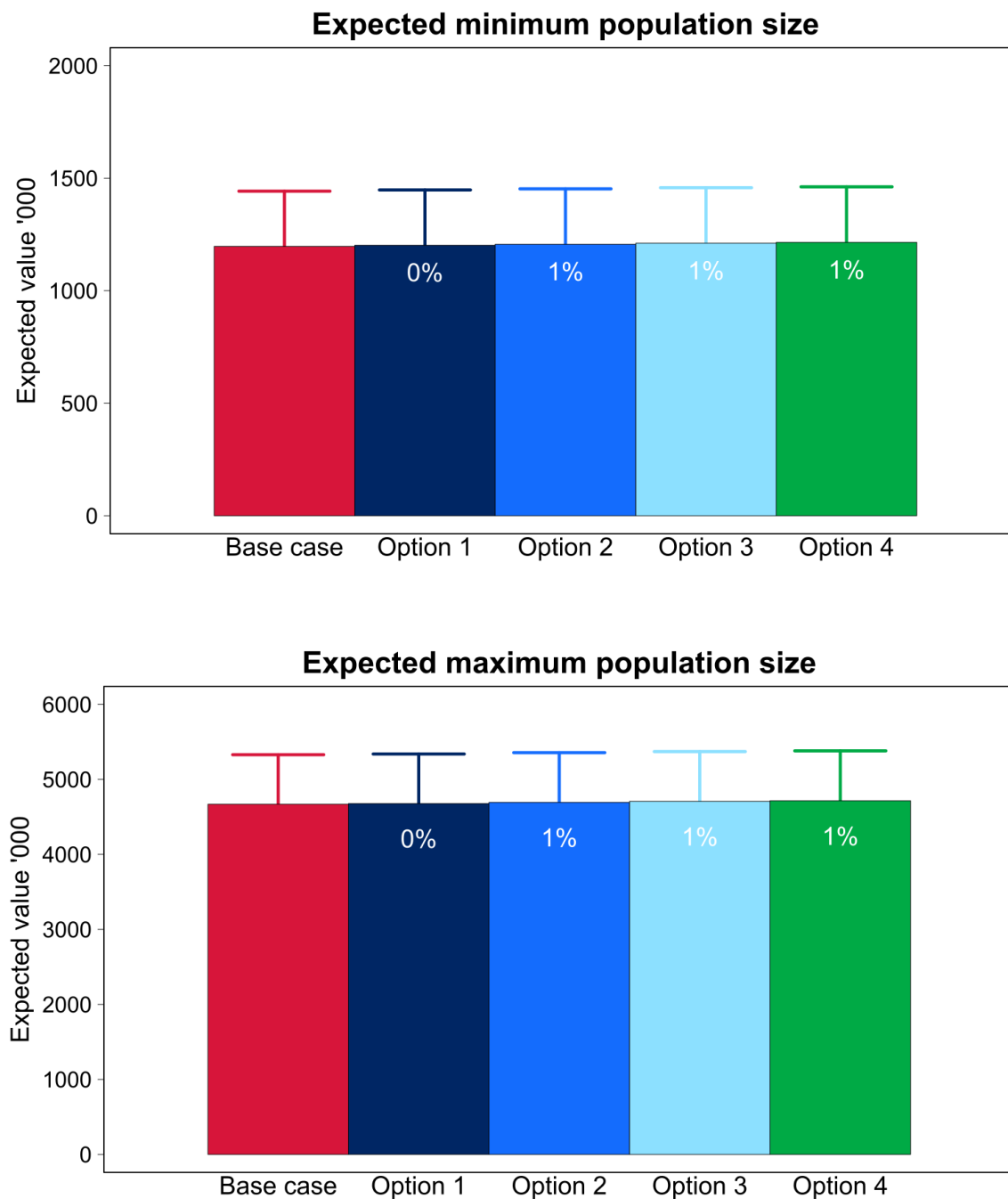


Figure A4.1. Modelled Carp adult population responses across all modelled reaches in the southern Murray–Darling Basin. Top panel: expected values of the minimum population size relative to the Base case, with percentage change from the Base case shown in each bar, and Bottom panel: expected values of the maximum population size relative to the Base case, with percentage change from the Base case shown in each bar. Minimum and maximum expected population sizes largely reflected the expected mean population size responses (see Results).

Total Murray River

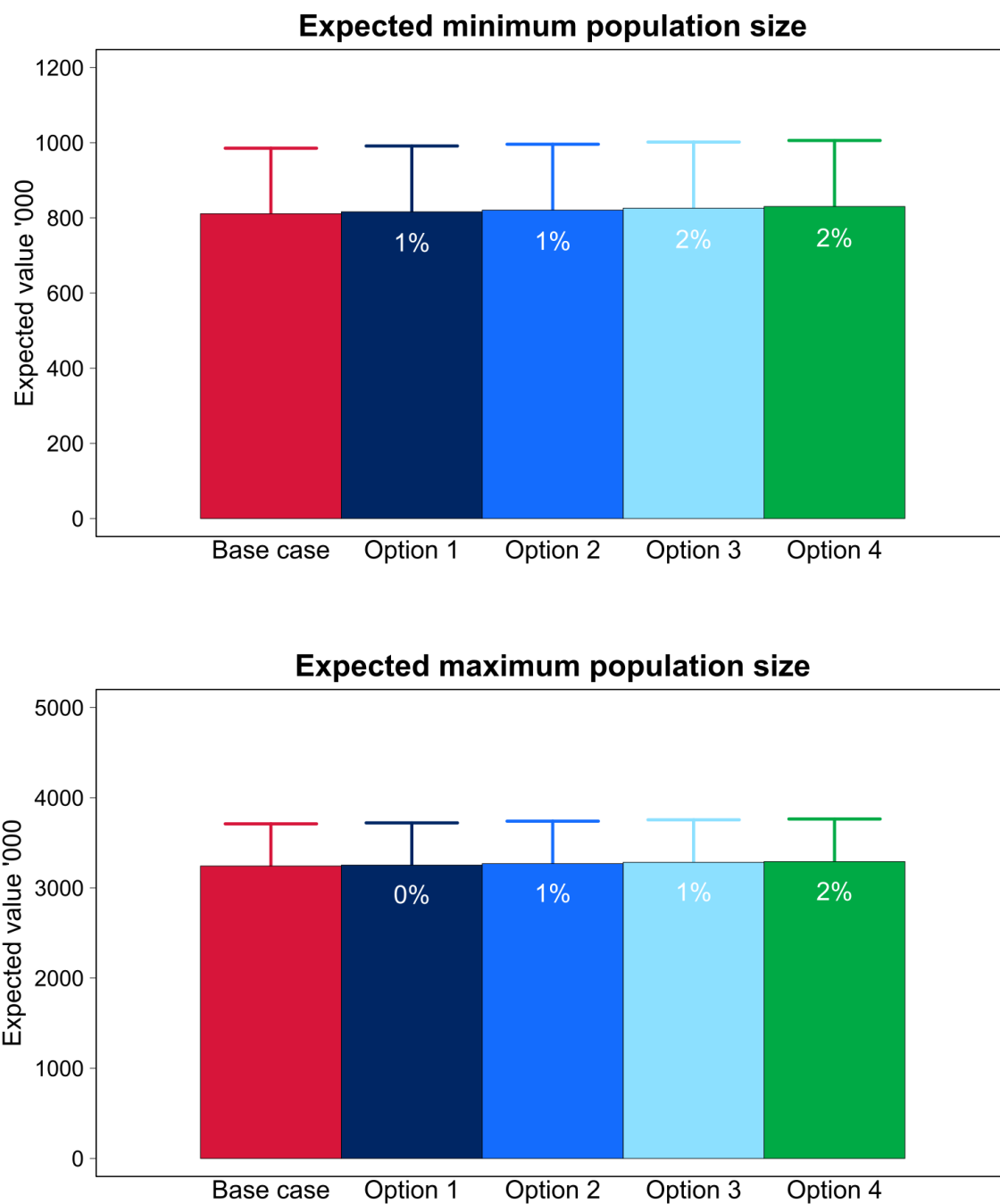


Figure A4.2. Modelled Carp adult population responses across all populations in the Murray River. Top panel: expected values of the minimum population size relative to the Base case, with percentage change from the Base case shown in each bar, and Bottom panel: expected values of the maximum population size relative to the Base case, with percentage change from the Base case shown in each bar. Minimum and maximum expected population sizes largely reflected the expected mean population size responses (see Results).

Total Murrumbidgee River

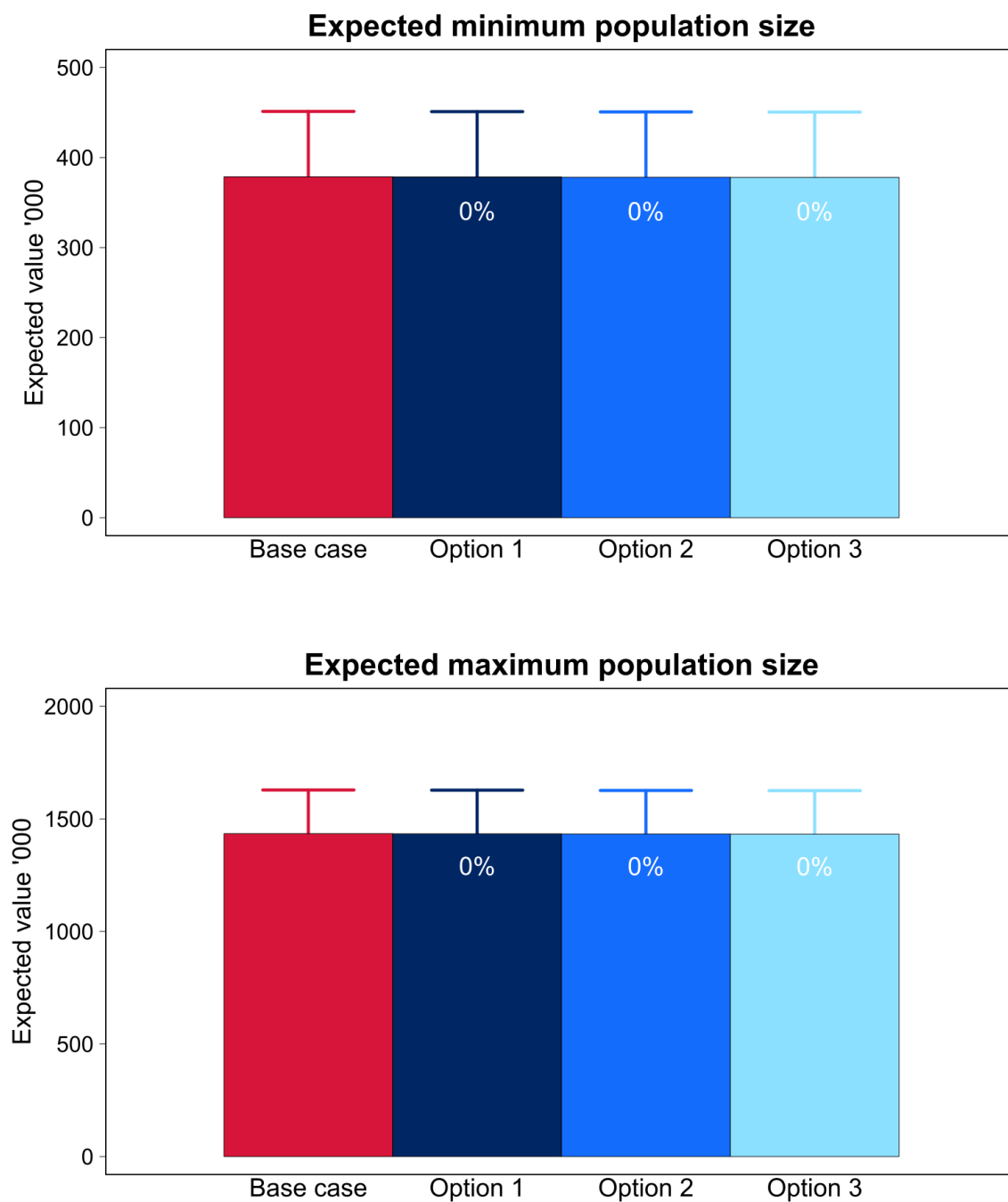


Figure A4.3. Modelled Carp adult population responses across all populations in the Murrumbidgee River. Top panel: expected values of the minimum population size relative to the Base case, with percentage change from the Base case shown in each bar, and Bottom panel: expected values of the maximum population size relative to the Base case, with percentage change from the Base case shown in each bar. Minimum and maximum expected population sizes largely reflected the expected mean population size responses (see Results).

Individual reach populations

Hume to Yarrawonga population

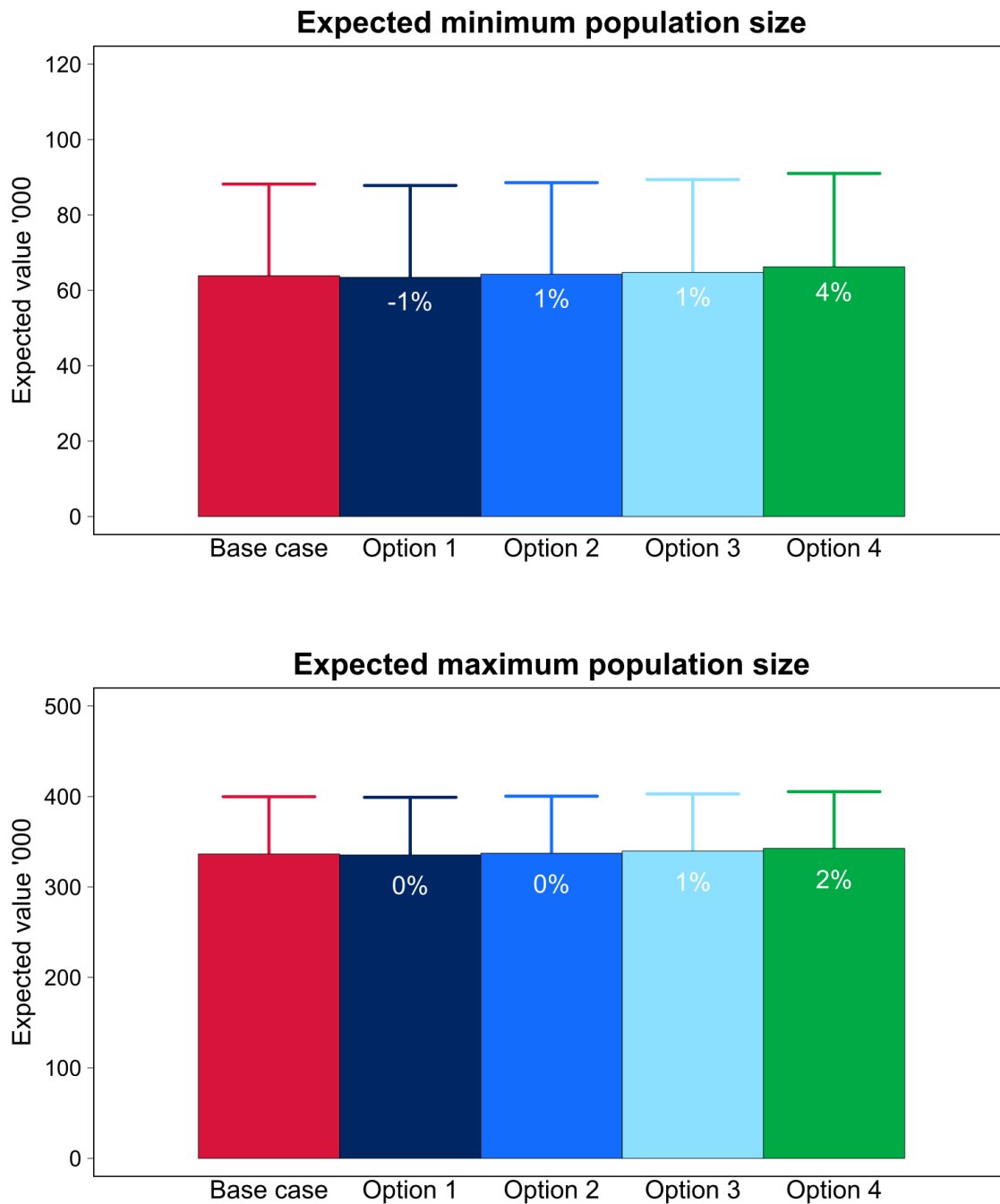


Figure A4.4. Modelled Carp adult population in the Hume to Yarrawonga reach (Murray River). Top panel: expected values of the minimum population size relative to the Base case, with percentage change from the Base case shown in each bar, and Bottom panel: expected values of the maximum population size relative to the Base case, with percentage change from the Base case shown in each bar. Minimum and maximum expected population sizes largely reflected the expected mean population size responses (see Results).

Yarrawonga to Torrumbarry population

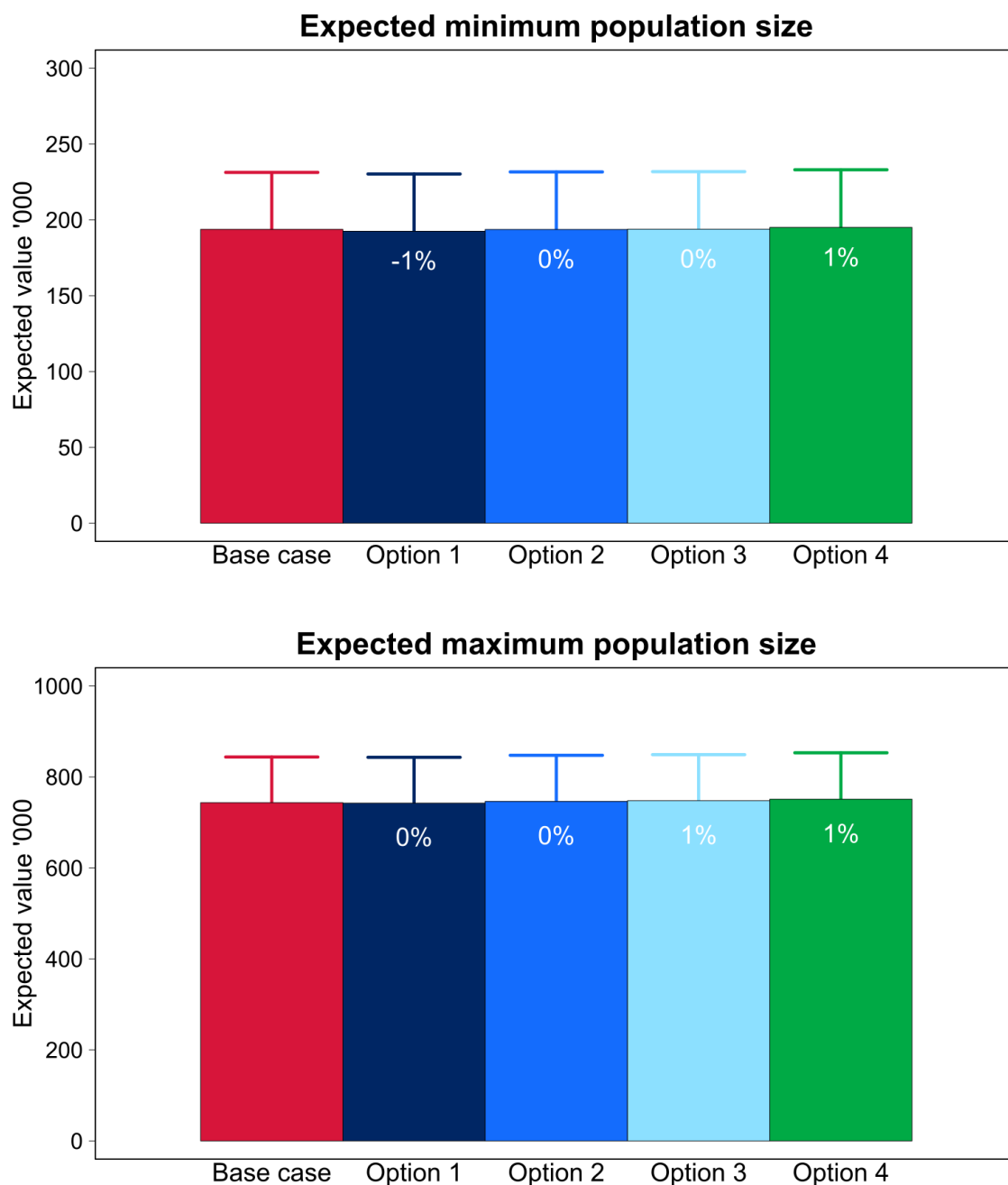
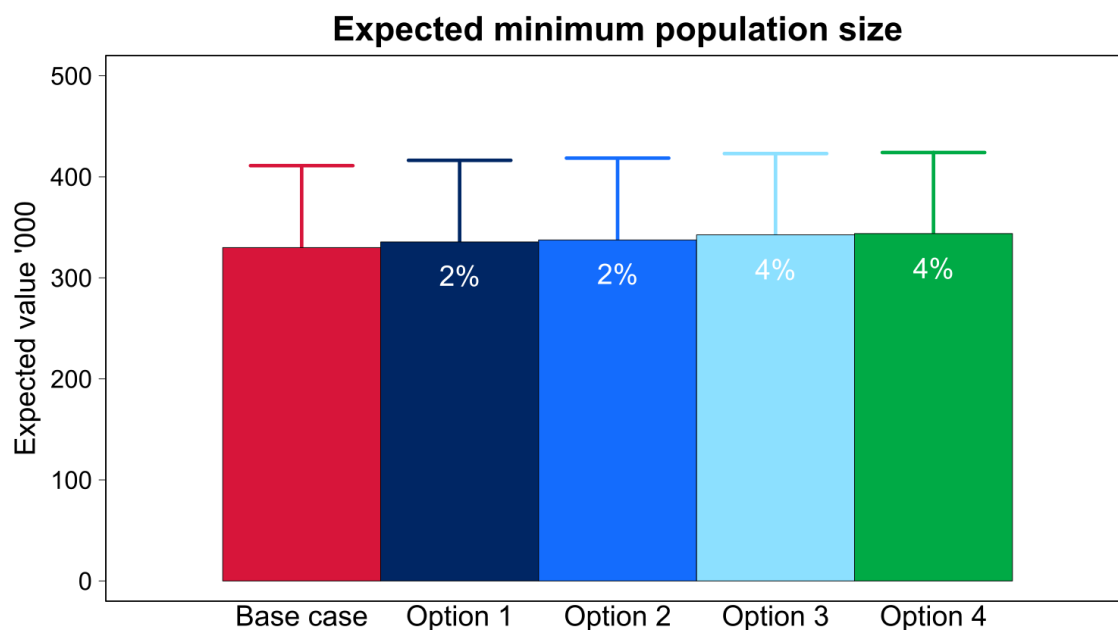


Figure A4.5. Modelled Carp adult population in the Yarrawonga to Torrumbarry reach (Murray River). Top panel: expected values of the minimum population size relative to the Base case, with percentage change from the Base case shown in each bar, and Bottom panel: expected values of the maximum population size relative to the Base case, with percentage change from the Base case shown in each bar. The similarity in population estimates is driven by the similarity in estimated floodplain area estimated by RiM-FIM/EW-FIM among hydrological flow scenarios. Minimum and maximum expected population sizes largely reflected the expected mean population size responses (see Results).

Torrumbarry to Wentworth population



4.

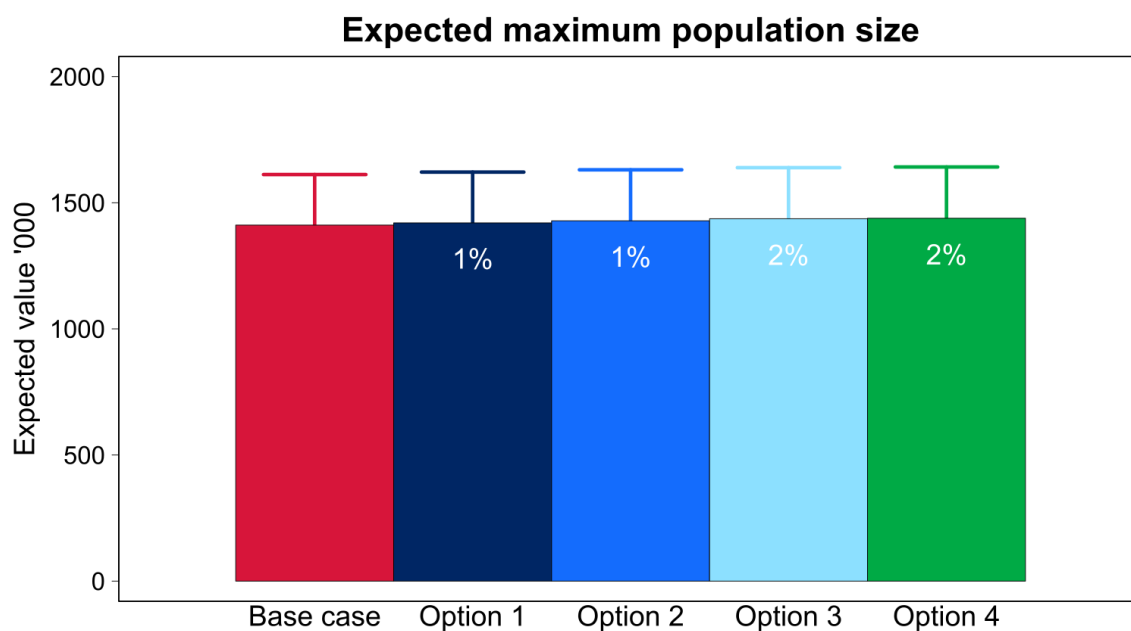


Figure A4.6. Modelled Carp adult population in the Torrumbarry to Wentworth reach (Murray River). Top panel: expected values of the minimum population size relative to the Base case, with percentage change from the Base case shown in each bar, and Bottom panel: expected values of the maximum population size relative to the Base case, with percentage change from the Base case shown in each bar. Minimum and maximum expected population sizes largely reflected the expected mean population size responses (see Results).

Edward River population

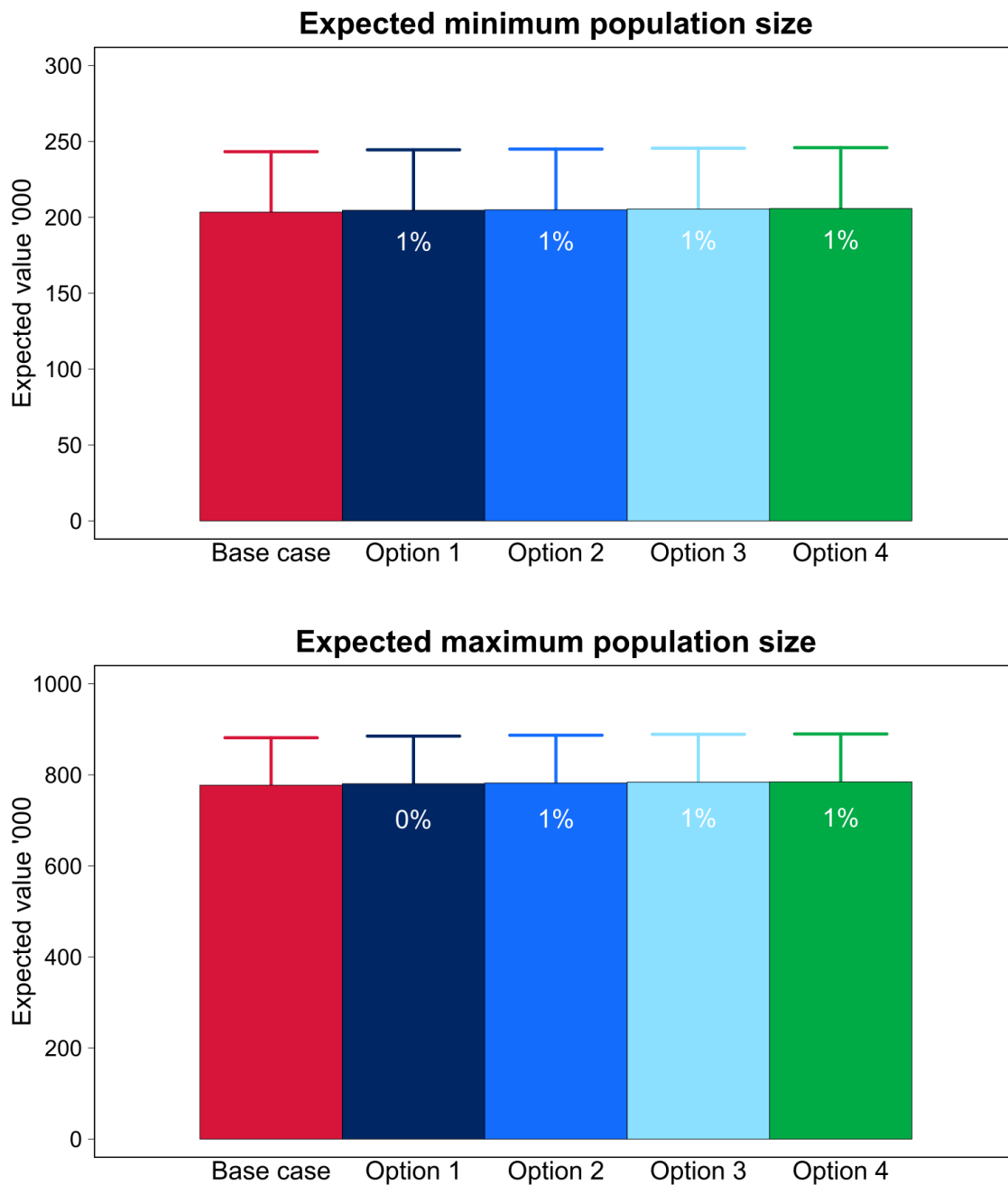


Figure A4.7. Modelled Carp adult population in the Edward River. Top panel: expected values of the minimum population size relative to the Base case, with percentage change from the Base case shown in each bar, and Bottom panel: expected values of the maximum population size relative to the Base case, with percentage change from the Base case shown in each bar. Minimum and maximum expected population sizes largely reflected the expected mean population size responses (see Results).

Gundagai to Hay population

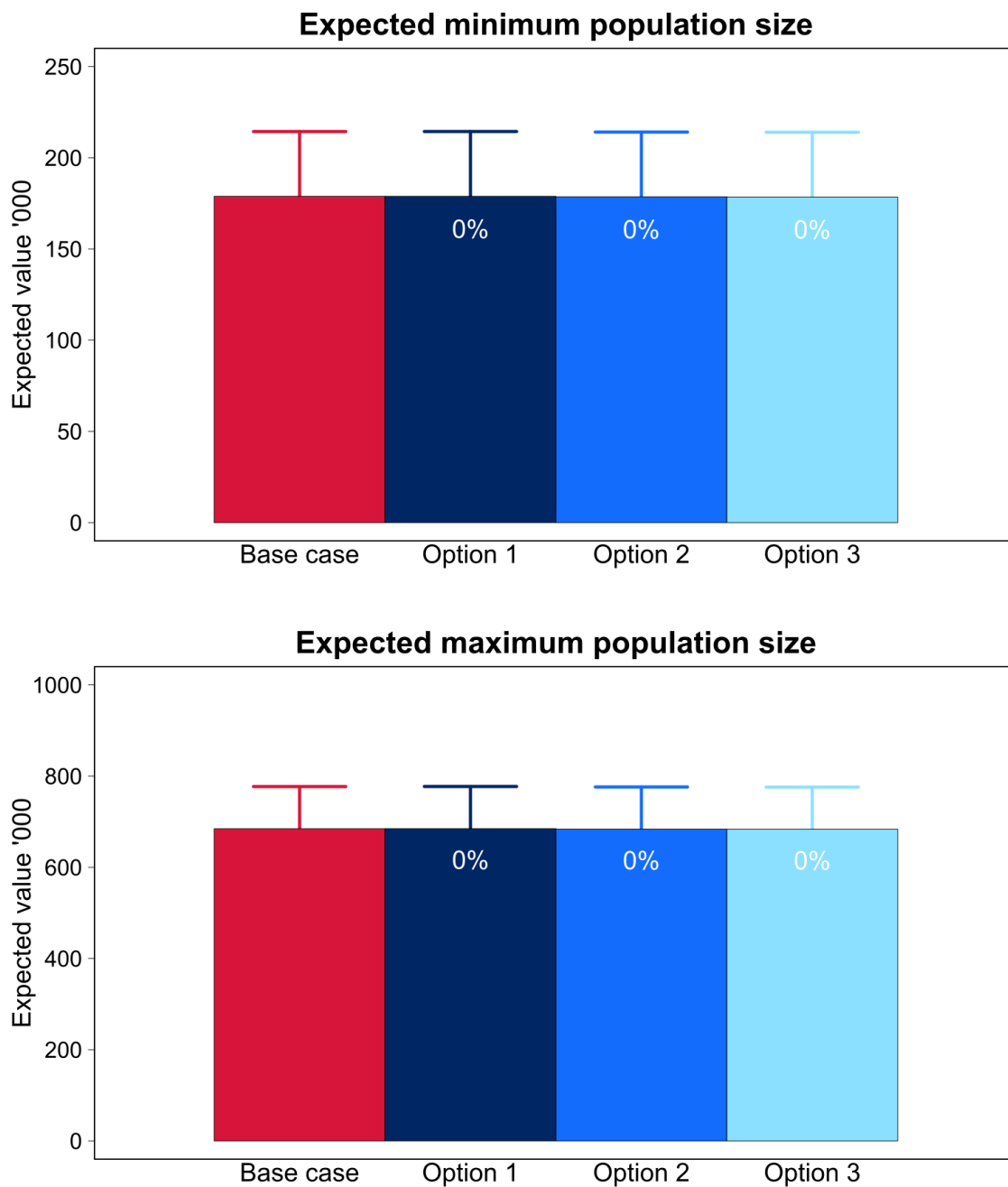


Figure A4.8. Modelled Carp adult population in the Gundagai to Hay reach (Murrumbidgee River). Top panel: expected values of the minimum population size relative to the Base case, with percentage change from the Base case shown in each bar, and Bottom panel: expected values of the maximum population size relative to the Base case, with percentage change from the Base case shown in each bar. Minimum and maximum expected population sizes largely reflected the expected mean population size responses (see Results).

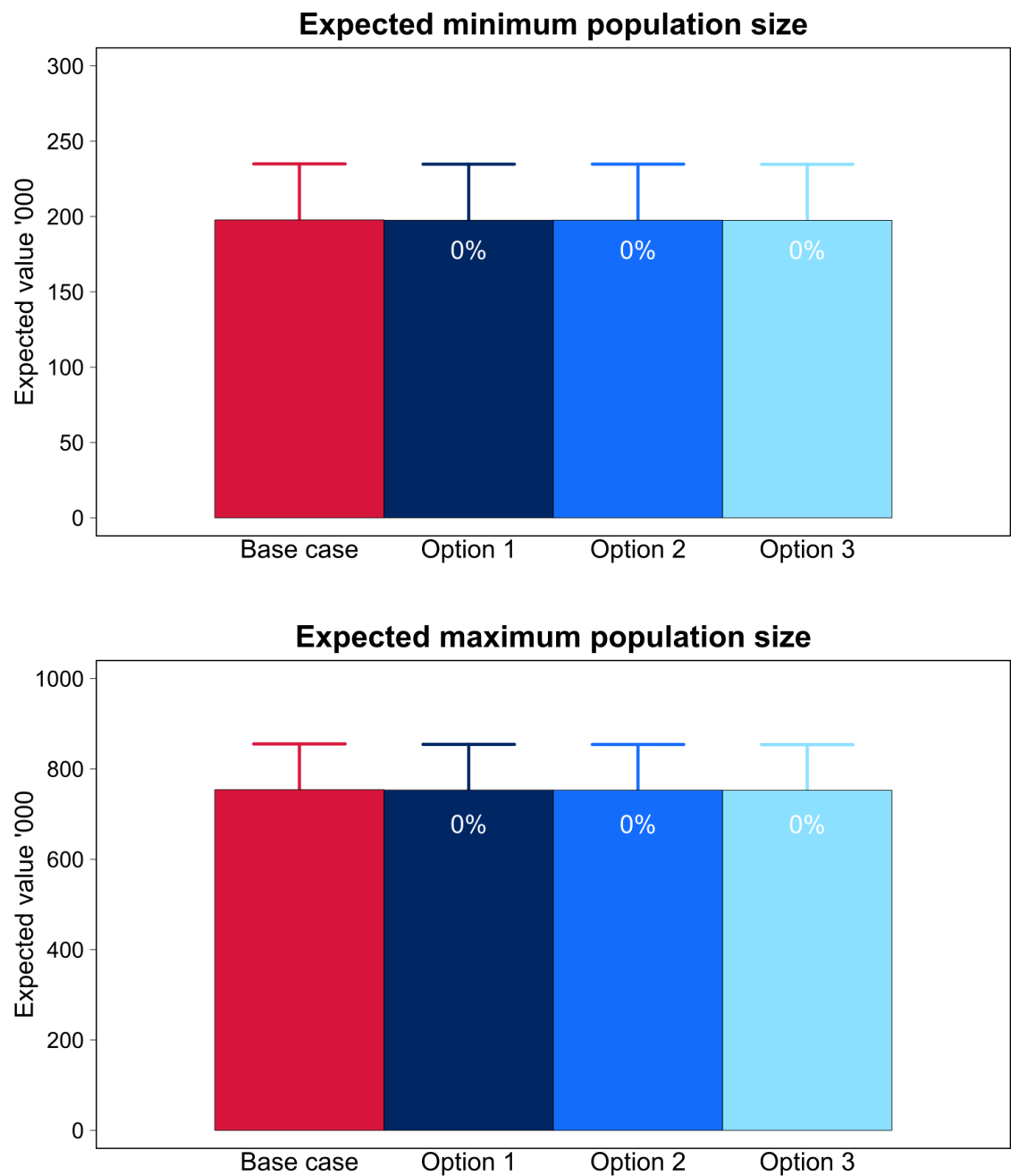


Figure A4.9. Modelled Carp adult population in the Hay to Balranald reach (Murrumbidgee River). Top panel: expected values of the minimum population size relative to the Base case, with percentage change from the Base case shown in each bar, and Bottom panel: expected values of the maximum population size relative to the Base case, with percentage change from the Base case shown in each bar. Minimum and maximum expected population sizes largely reflected the expected mean population size responses (see Results).

Adult Carp expected minimum and maximum population sizes for the years 1990–2019

Total populations

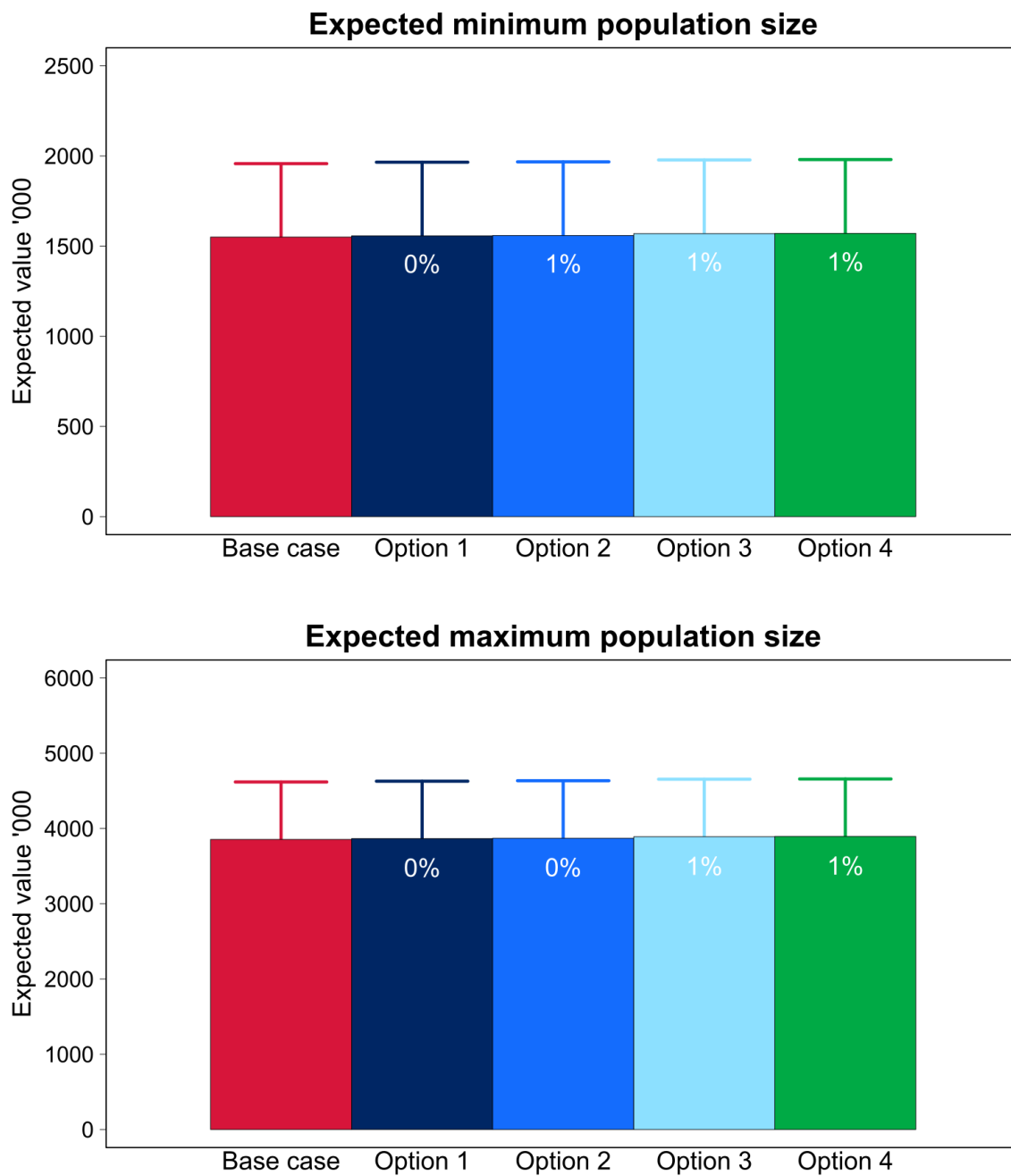


Figure A4.10. Modelled Carp adult population responses across all modelled reaches in the southern Murray–Darling Basin for the years 1990–2019. Top panel: expected values of the minimum population size relative to the Base case, with percentage change from the Base case shown in each bar, and Bottom panel: expected values of the maximum population size relative to the Base case, with percentage change from the Base case shown in each bar.

Early life-history responses of Carp

Total populations

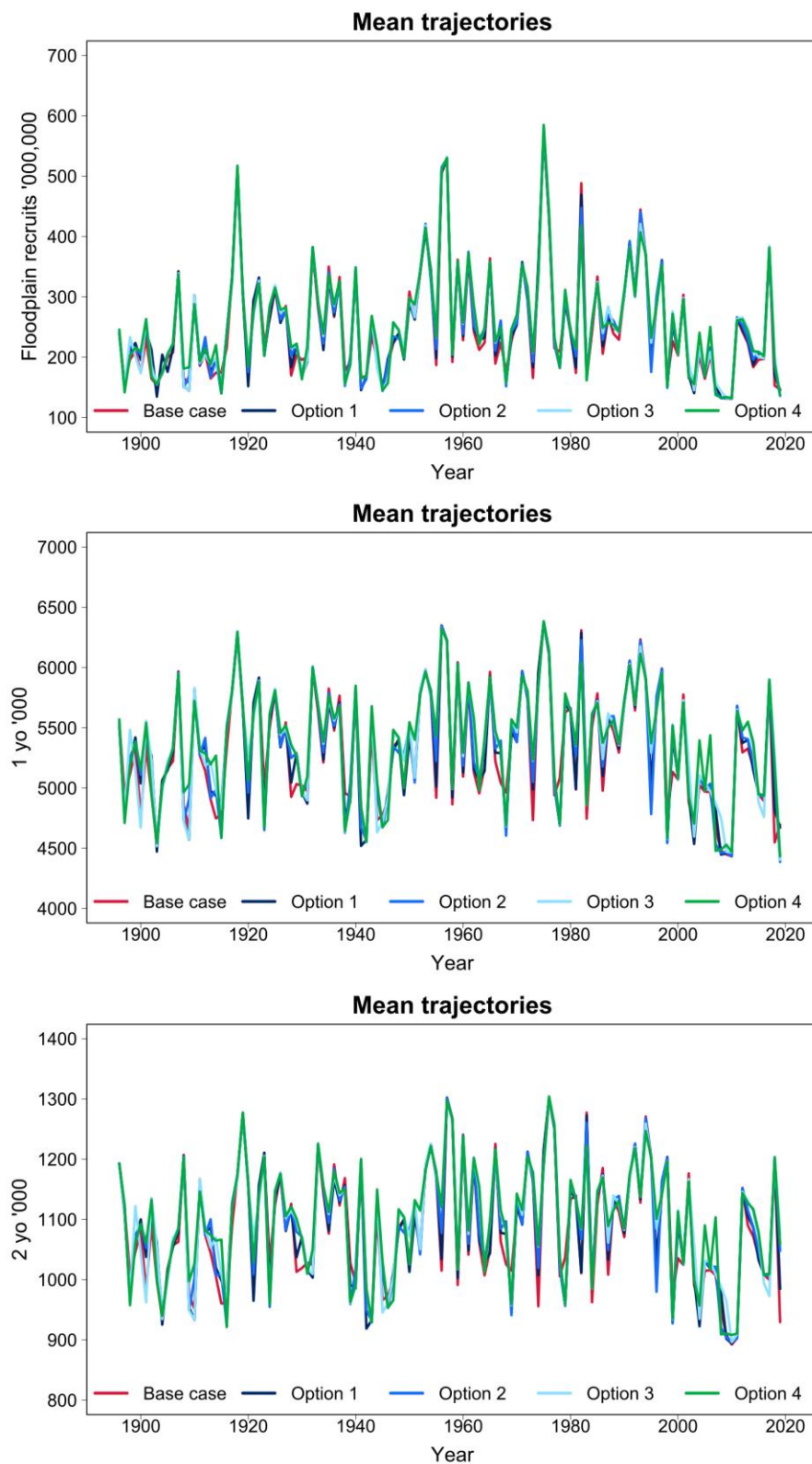


Figure A4.11. Predicted early life-history responses of Carp across all modelled program reaches in the southern Murray–Darling Basin. Lines show the Base case trajectories compared to flow scenarios 1–4. Top panel shows mean floodplain recruit (fingerlings) trajectories. Middle panel shows mean 1-year-old trajectories and the bottom panel shows 2-year-old trajectories. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Total Murray River

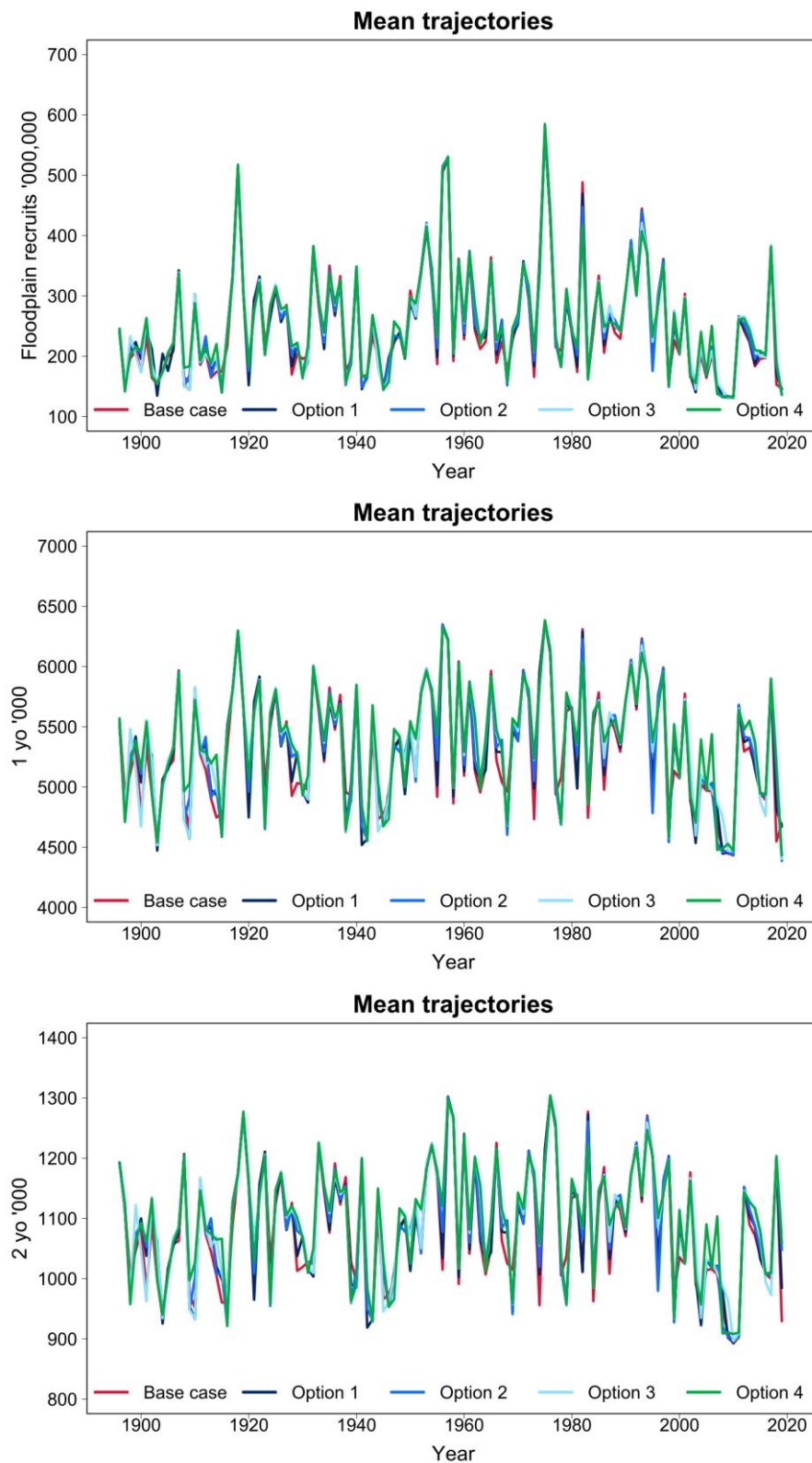


Figure A4.12. Predicted early life-history responses of Carp across all modelled reaches in the Murray River (including the Edward River). Lines show the Base case trajectories compared to flow scenarios 1–4. Top panel shows mean floodplain recruit (fingerlings) trajectories. Middle panel shows mean 1-year-old trajectories, and the bottom panel shows 2-year-old trajectories. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Total Murrumbidgee River

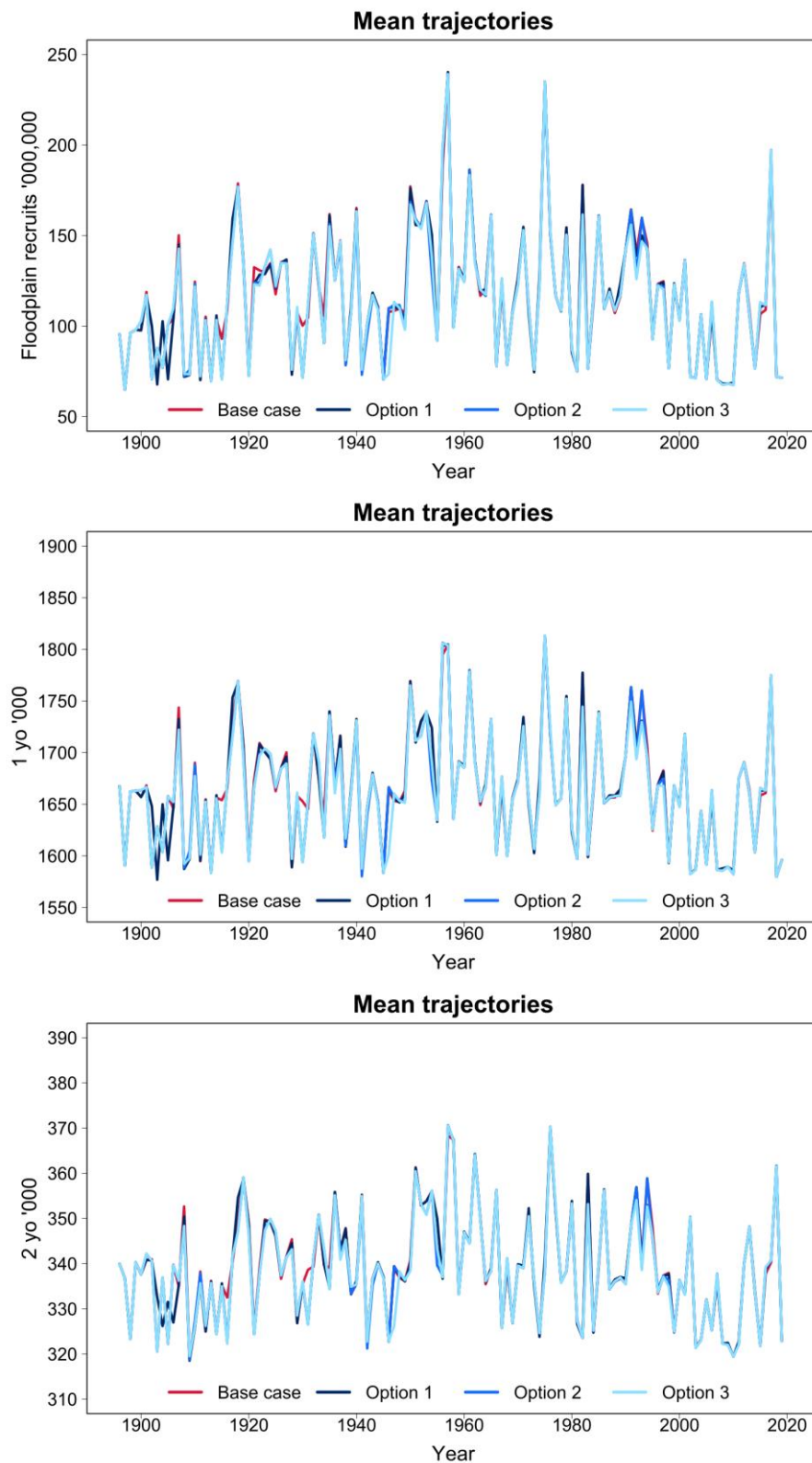


Figure A4.13. Predicted early life-history responses of Carp across both modelled reaches in the Murrumbidgee River. Lines show the Base case trajectories compared to flow scenarios 1–4. Top panel shows mean floodplain recruit (fingerlings) trajectories. Middle panel shows mean 1-year-old trajectories, and the bottom panel shows 2-year-old trajectories. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Individual reach populations

Hume to Yarrawonga population

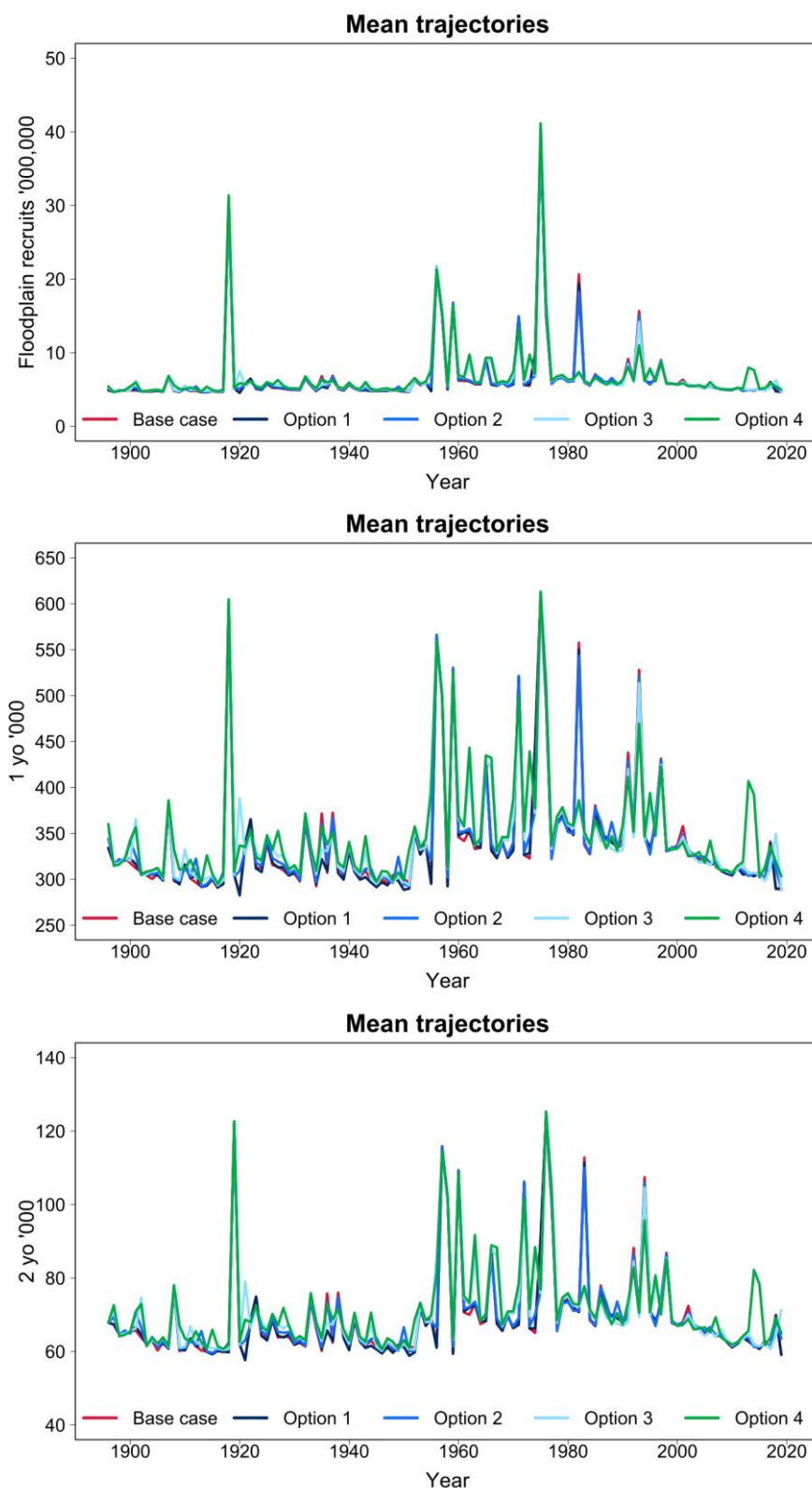


Figure A4.14. Predicted early life-history responses of Carp in the Hume to Yarrawonga reach (Murray River). Lines show the Base case trajectories compared to flow scenarios 1–4. Top panel shows mean floodplain recruit (fingerlings) trajectories. Middle panel shows mean 1-year-old trajectories, and the bottom panel shows 2-year-old trajectories. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Yarrawonga to Torrumbarry population

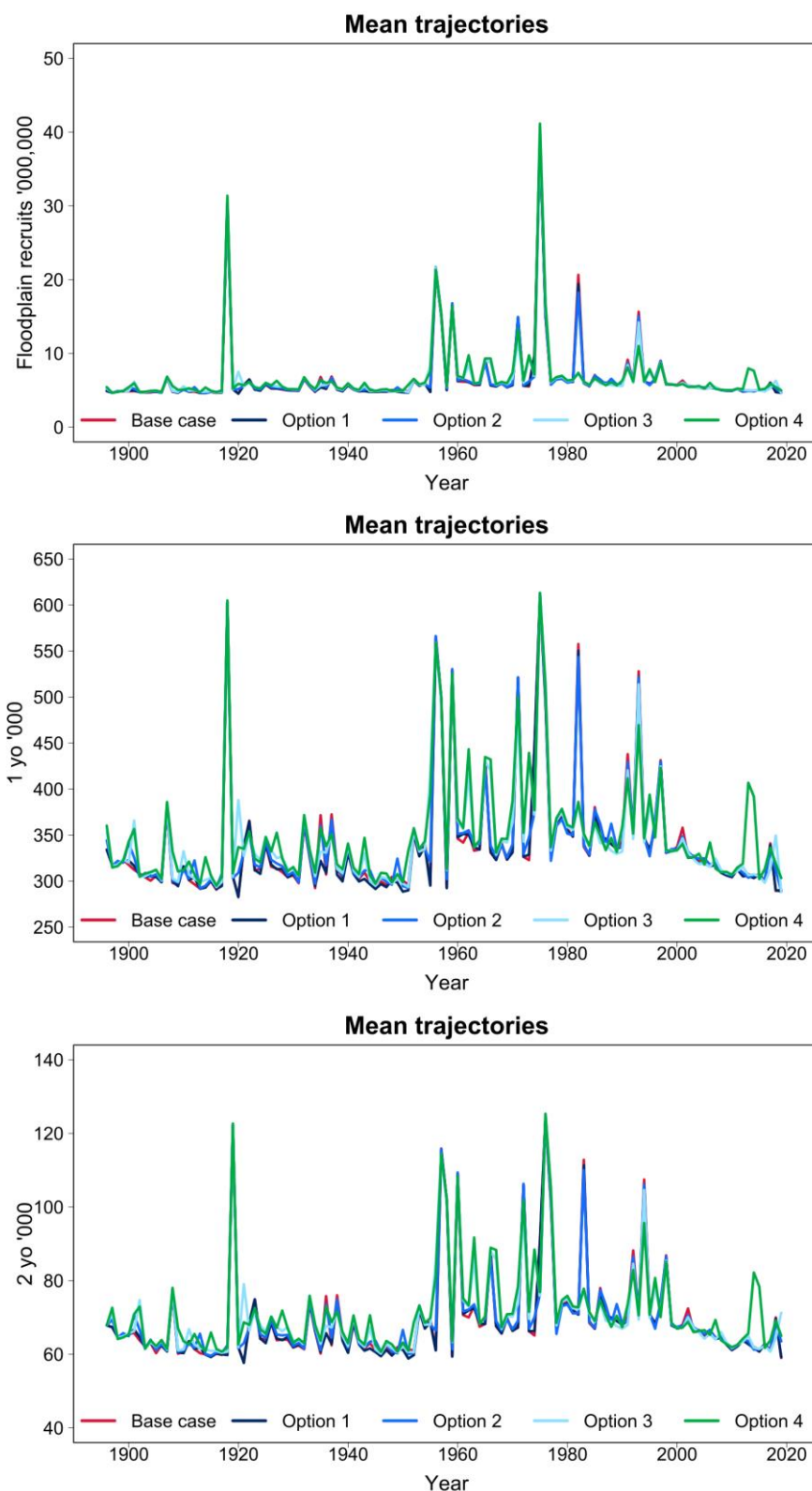


Figure A4.15. Predicted early life-history responses of Carp in the Yarrawonga to Torrumbarry reach (Murray River). Lines show the Base case trajectories compared to flow scenarios 1–4. Top panel shows mean floodplain recruit (fingerlings) trajectories. Middle panel shows mean 1-year-old trajectories, and the bottom panel shows 2-year-old trajectories. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Torrumbarry to Wentworth population

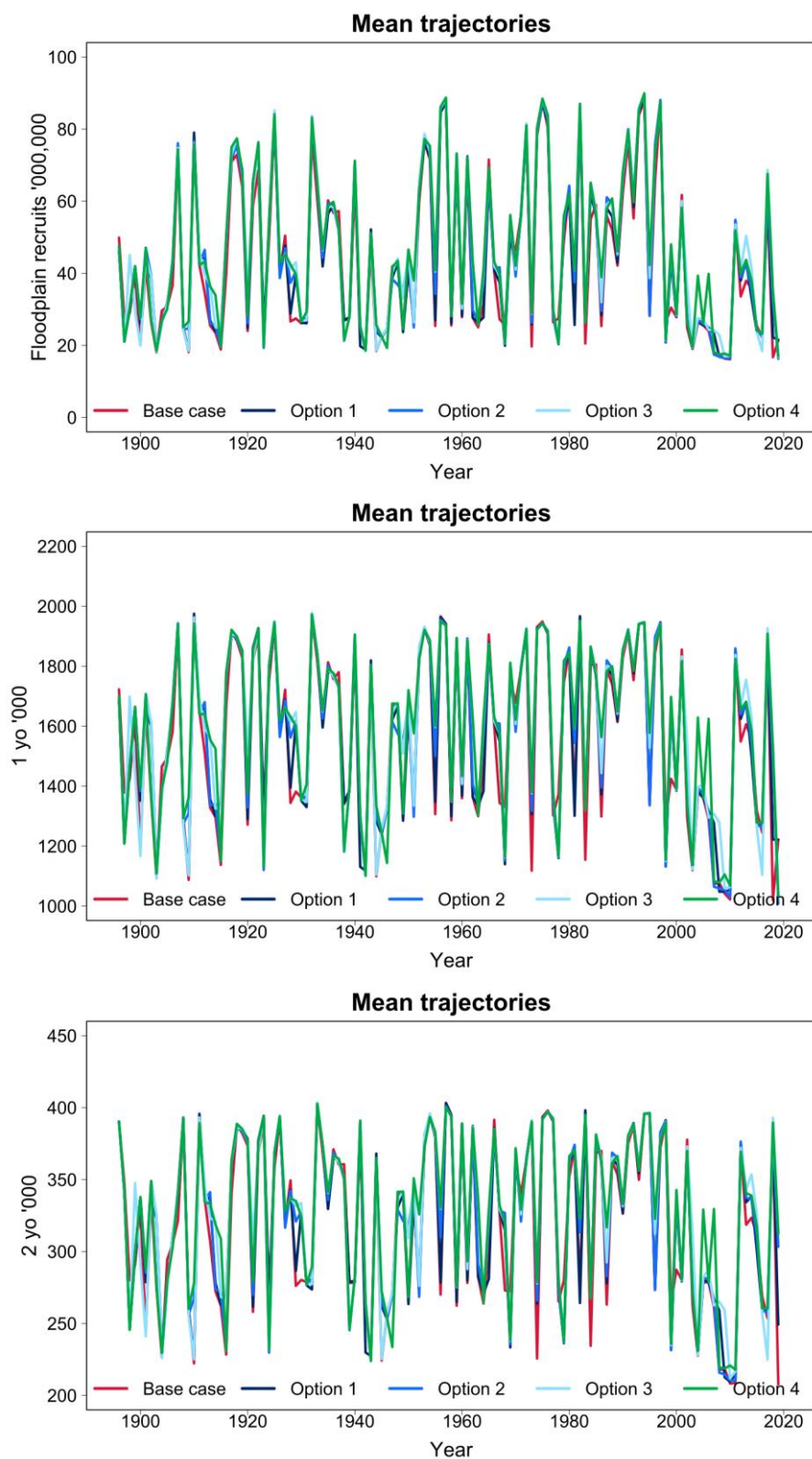


Figure A4.16. Predicted early life-history responses of Carp in the Torrumbarry to Wentworth reach (Murray River). Lines show the Base case trajectories compared to flow scenarios 1–4. Top panel shows mean floodplain recruit (fingerlings) trajectories. Middle panel shows mean 1-year-old trajectories, and the bottom panel shows 2-year-old trajectories. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Edward River population

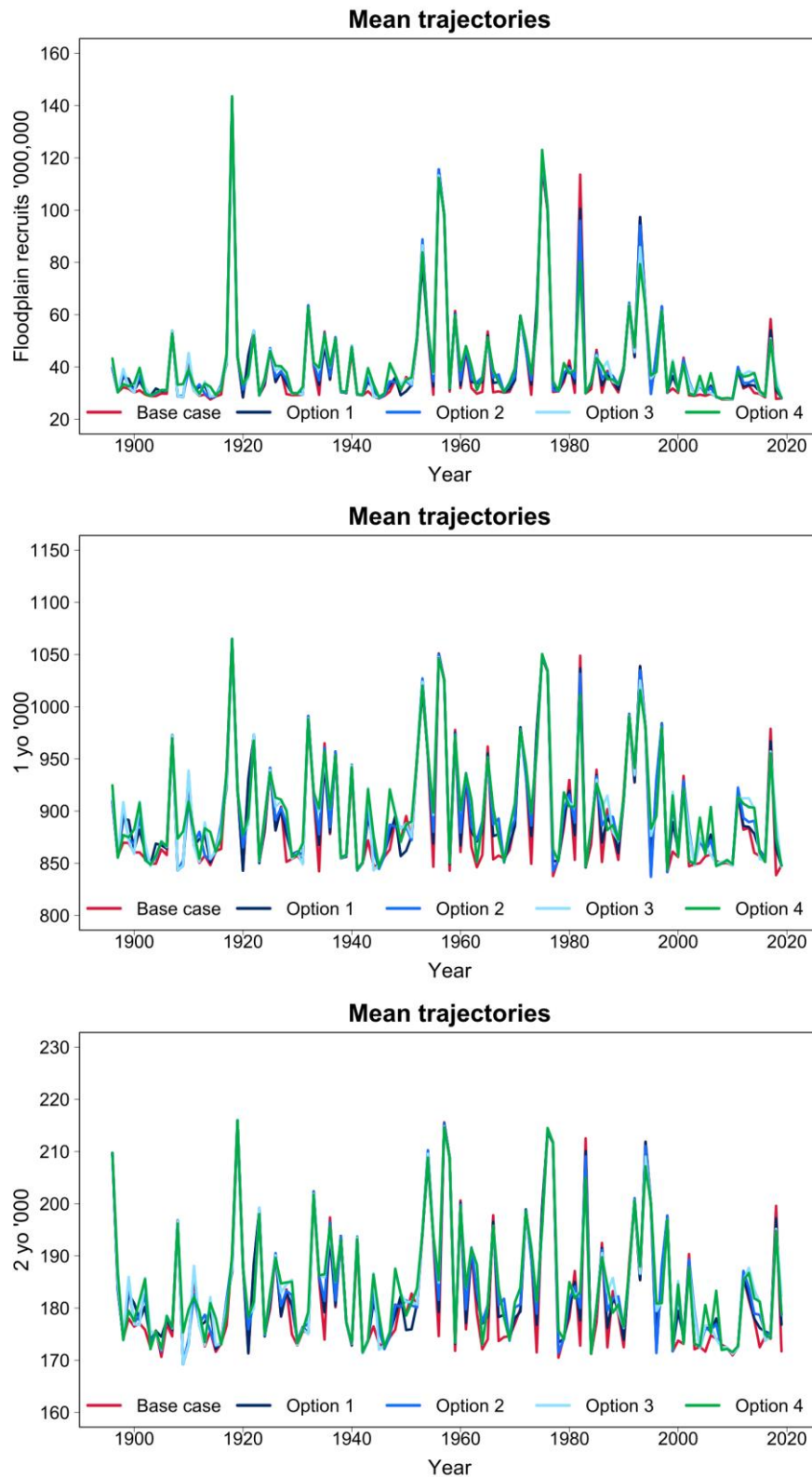


Figure A4.17. Predicted early life-history responses of Carp in the Edward River. Lines show the Base case trajectories compared to flow scenarios 1–4. Top panel shows mean floodplain recruit (fingerlings) trajectories. Middle panel shows mean 1-year-old trajectories, and the bottom panel shows 2-year-old trajectories. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Gundagai to Hay population

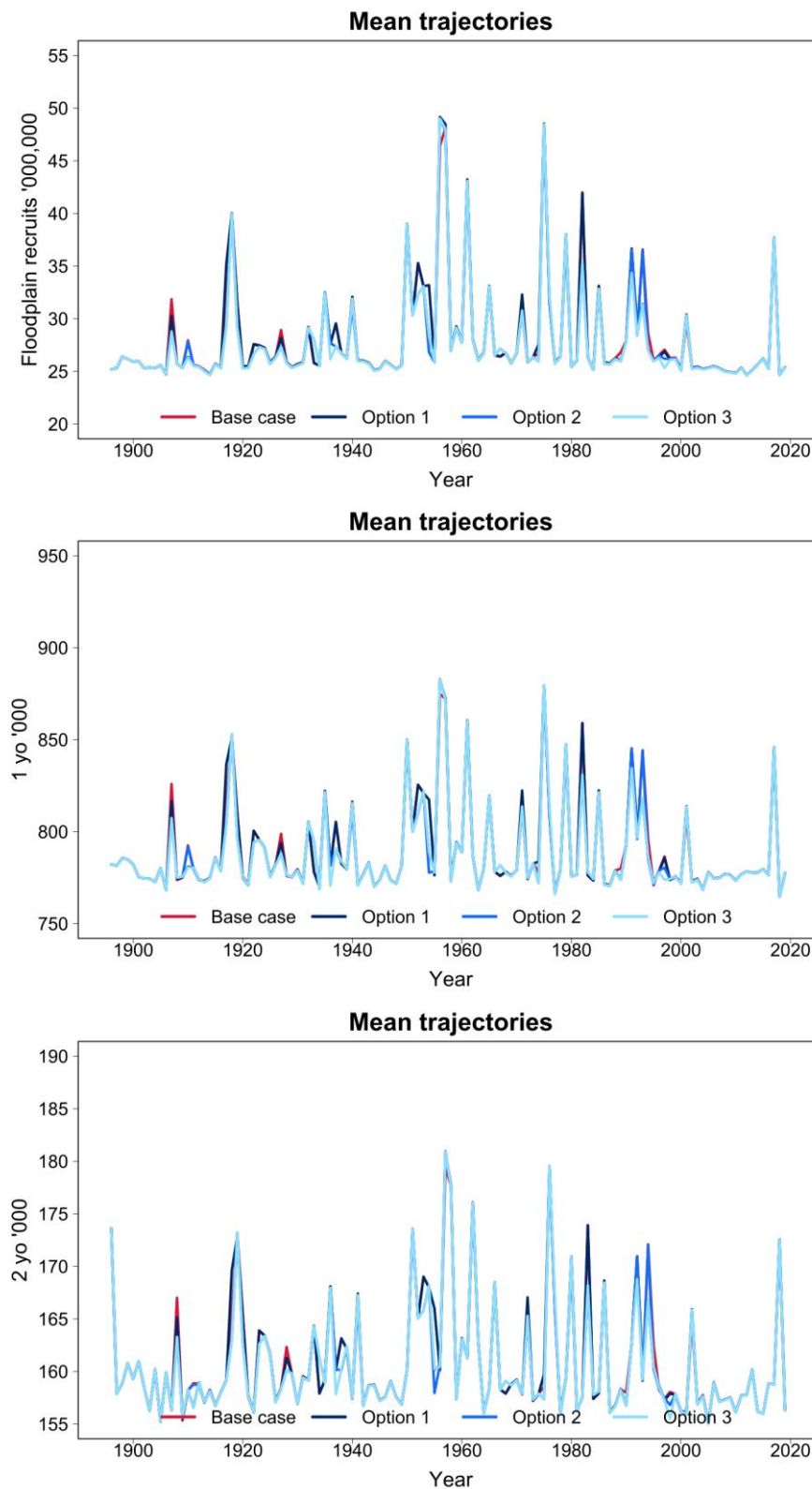


Figure A4.18. Predicted early life-history responses of Carp in the Gundagai to Hay reach (Murrumbidgee River). Lines show the Base case trajectories compared to flow scenarios 1–4. Top panel shows mean floodplain recruit (fingerlings) trajectories. Middle panel shows mean 1-year-old trajectories, and the bottom panel shows 2-year-old trajectories. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Hay to Balranald population

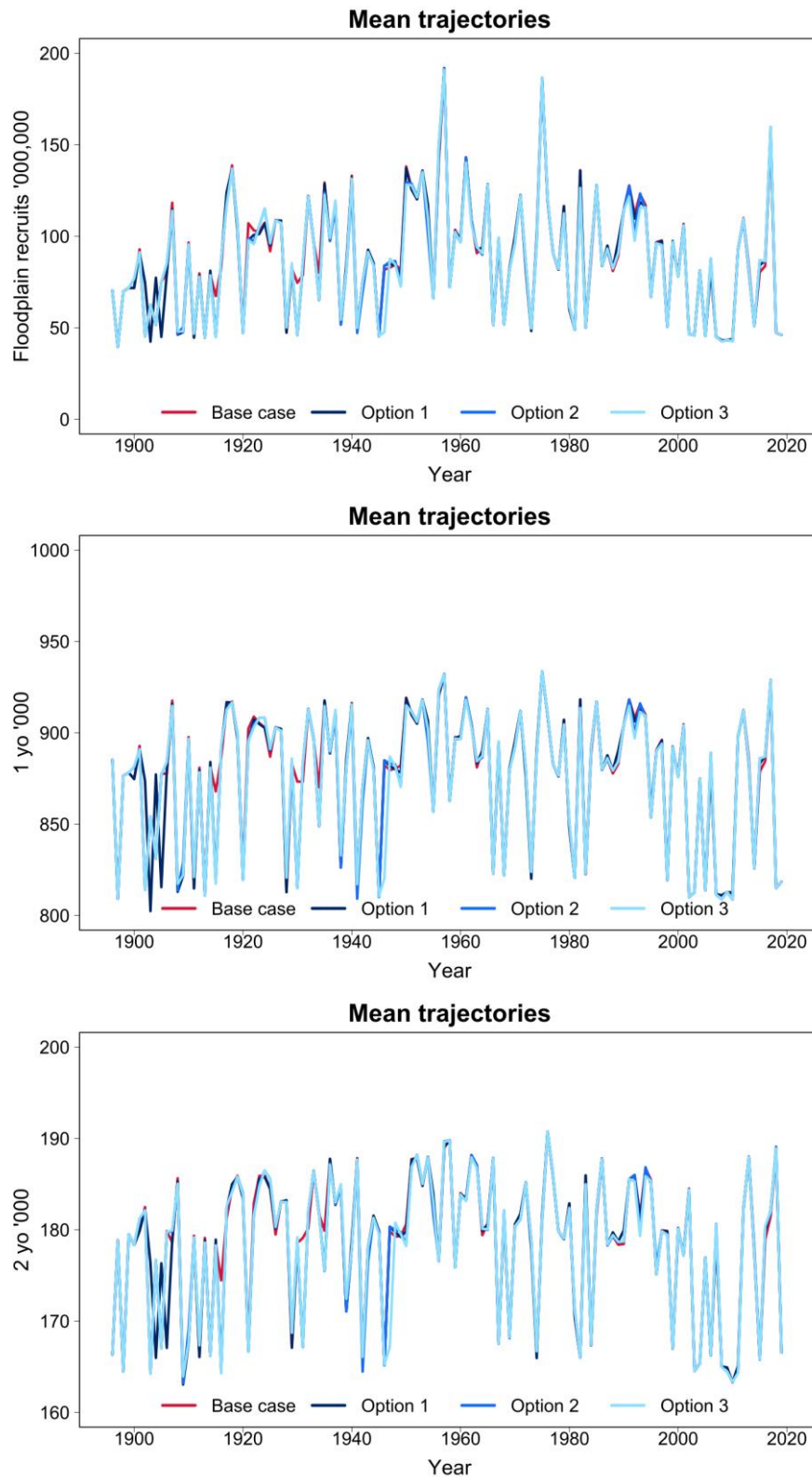


Figure A4.19. Predicted early life-history responses of Carp in the Hay to Balranald reach (Murrumbidgee River). Lines show the Base case trajectories compared to flow scenarios 1–4. Top panel shows mean floodplain recruit (fingerlings) trajectories. Middle panel shows mean 1-year-old trajectories, and the bottom panel shows 2-year-old trajectories. Note that the Carp population predictions are presented for the entire flow-time series (1896–2019) to provide a sense of their dynamism through time even though Carp did not invade the MDB until the late 1960s.

Early life-history responses of Carp for the years 1990–2019

Total populations

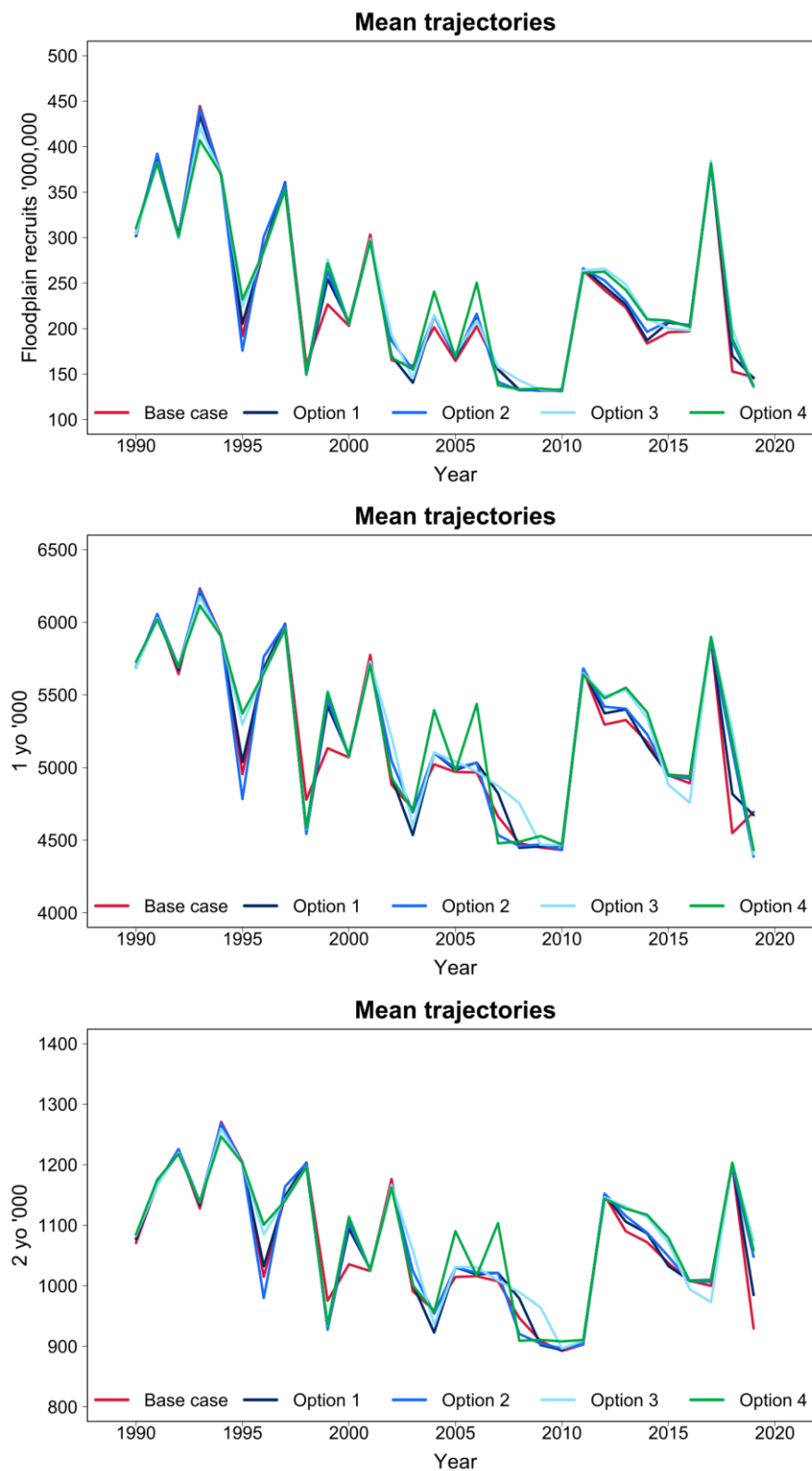


Figure A4.20. Predicted early life-history responses of Carp across all modelled program reaches in the southern Murray–Darling Basin for the years 1990–2019. Lines show the Base case trajectories compared to flow scenarios 1–4. Top panel shows mean floodplain recruit (fingerlings) trajectories. Middle panel shows mean 1-year-old trajectories, and the bottom panel shows 2-year-old trajectories.

Model sensitivity to assumptions about attractiveness of inundated floodplain habitats to Carp

Hume to Yarrawonga

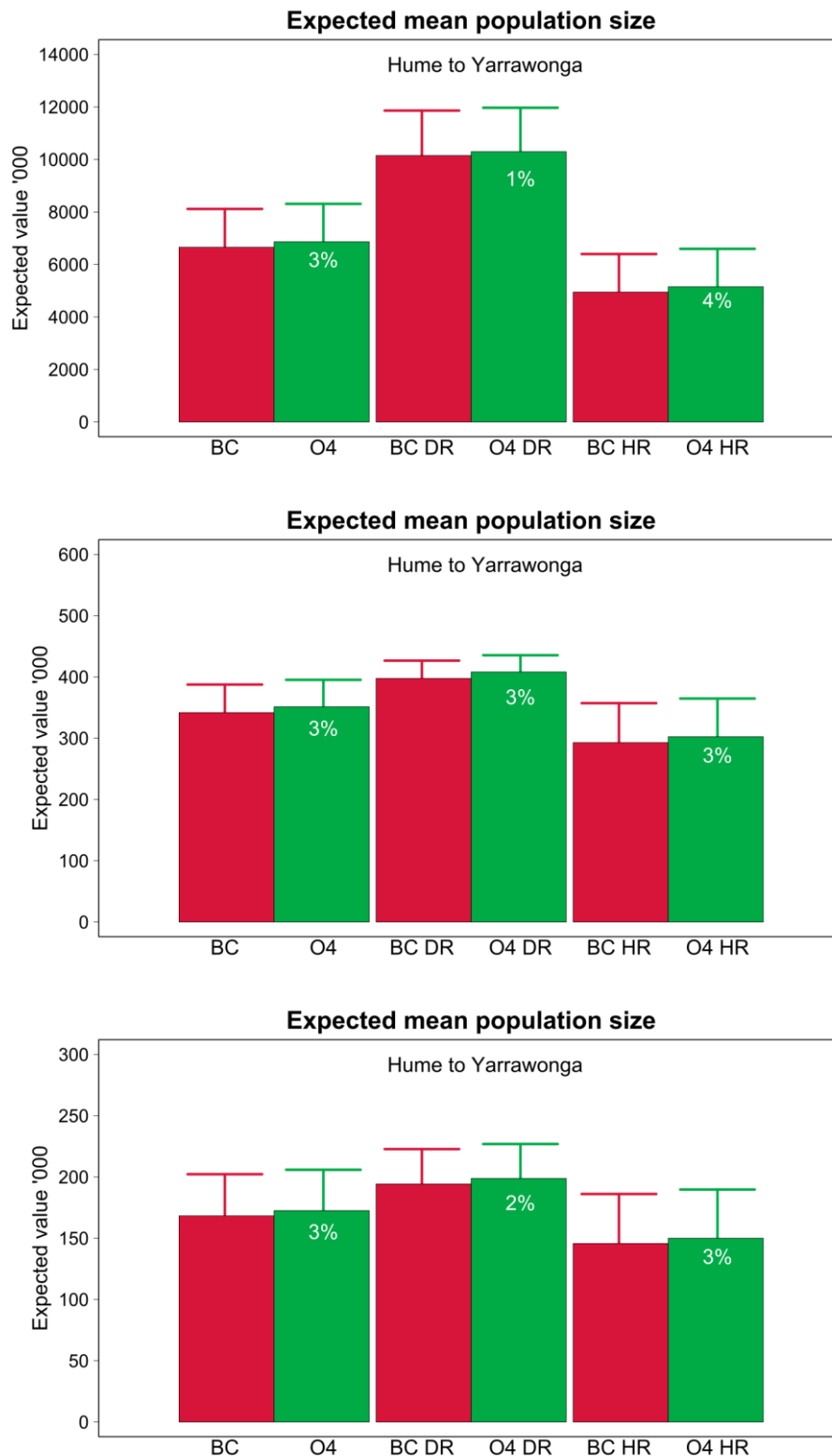


Figure A4.21. Hume to Yarrawonga expected values of the mean population size for the Base case (BC) and Option 4 (O4) for modelled Carp access to the floodplain, double rate of access to the floodplain (DR), and half rate of access to the floodplain (HR). Percentage change from the relevant Base case shown in each bar: top panel floodplain recruits; middle panel one-year-olds; bottom panel adults.

Yarrawonga to Torrumbarry

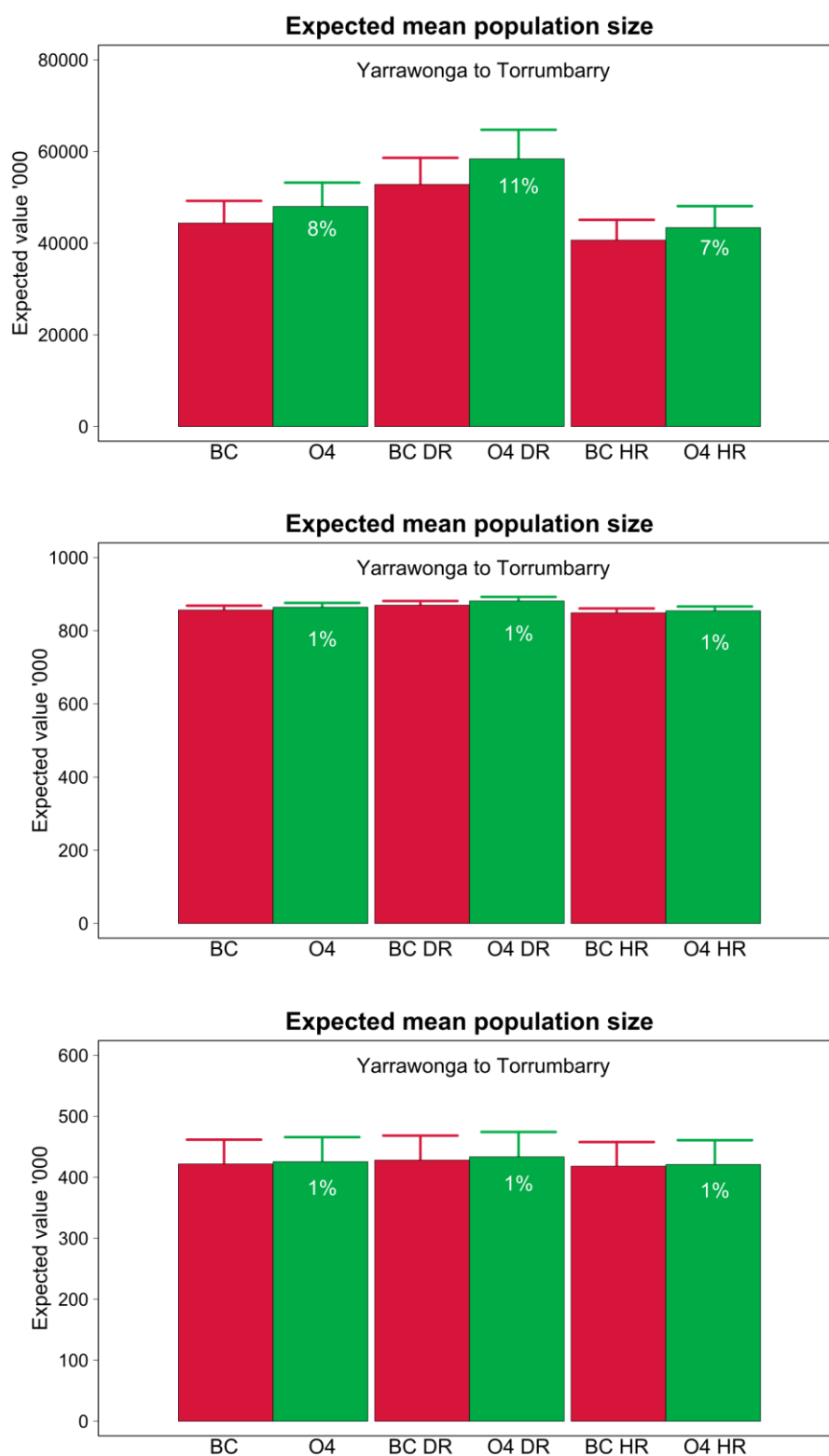


Figure A4.22. Yarrawonga to Torrumbarry expected values of the mean population size for the Base case (BC) and Option 4 (O4) for modelled Carp access to the floodplain, double rate of access to the floodplain (DR), and half rate of access to the floodplain (HR). Percentage change from the relevant Base case shown in each bar: top panel floodplain recruits; middle panel one-year-olds; bottom panel adults.

Edward River

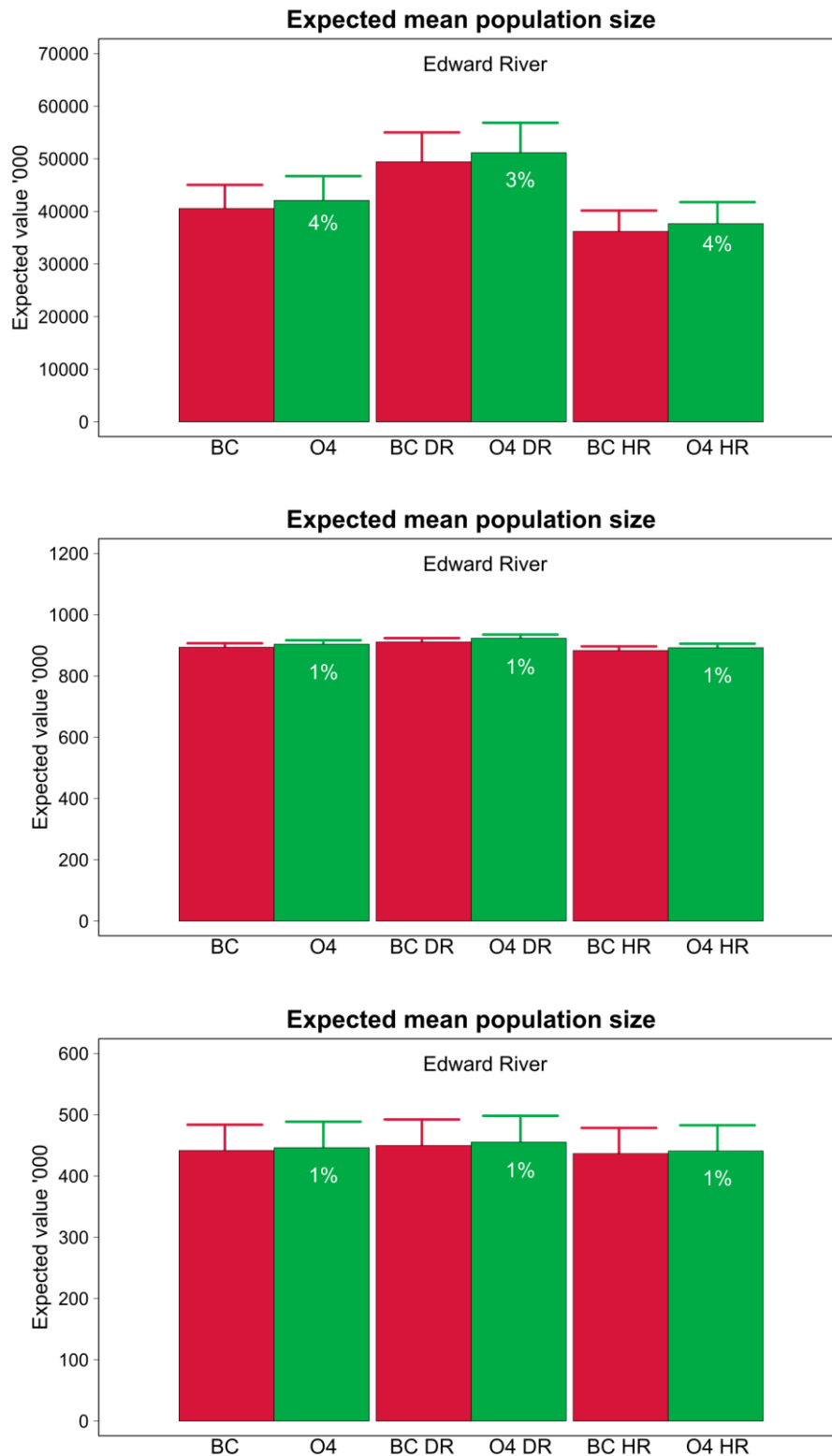


Figure A4.23. Edward River expected values of the mean population size for the Base case (BC) and Option 4 (O4) for modelled Carp access to the floodplain, double rate of access to the floodplain (DR), and half rate of access to the floodplain (HR). Percentage change from the relevant Base case shown in each bar: top panel floodplain recruits; middle panel one-year-olds; bottom panel adults.

Hay to Balranald

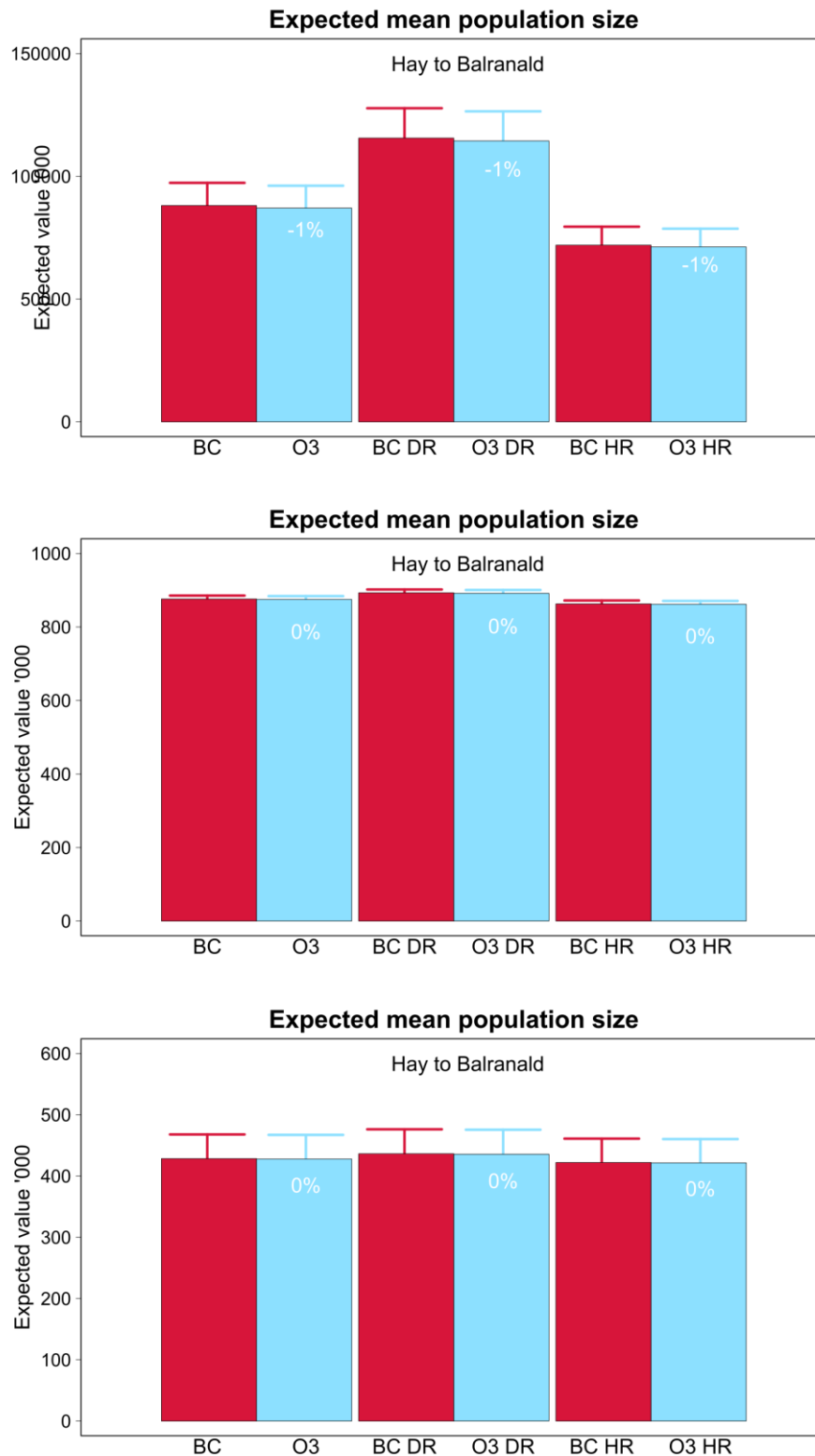


Figure A4.24. Hay to Balranald expected values of the mean population size for the Base case (BC) and Option 4 (O4) for modelled Carp access to the floodplain, double rate of access to the floodplain (DR), and half rate of access to the floodplain (HR). Percentage change from the relevant Base case shown in each bar: top panel floodplain recruits; middle panel one-year-olds; bottom panel adults.

Sensitivity analysis of the different habitat types available as a means of exploring sensitivity to alternative configurations of early life-history survival

The results of the sensitivity, elasticity and reproductive value analyses for the range of estimated early life-history stage (ELHS) survival rates encompassing the different aquatic habitat types (Table A2.1 and Table A3.1) have been presented in Figure A4.25–Figure A4.38. The various configurations of different ELHS survival rates in Table A3.1 allow for a ranging sensitivity analysis of the effects of ELHS variation population dynamics. Without exception, the model is most sensitive to changes in 1-year-old survival rates, regardless of ELHS configuration, though the strength depends on the ELHS configuration. The survival rate elasticity pattern is similar across habitat types with 1-year-old and 2-year-old elasticity values being equal, and then subsequently decays with the decay rate dependent on the growth rate (compare Figure A4.25–Figure A4.38). For habitat types with a population growth rate < 1 (see Table A3.1), elasticity analysis indicated that the model was largely insensitive to proportional change in ELHS survival rates and fecundity, and the distribution of the age class reproductive values was skewed to the right (Figure A4.25, Figure A4.26, Figure A4.28, and Figure A4.38). This indicates that young adults contribute significantly more than older Carp to future generations. For habitat types with a population growth rate > 1 , elasticity analysis was most sensitive to juvenile survival rates, though the effect of proportional change remained low (Figure A4.27, Figure A4.29–Figure A4.37). Elasticity analysis of fecundity demonstrated that the population growth rate was insensitive to changes in fecundity, though with increasing growth rate, there was an increase (albeit small) in sensitivity to fecundity of young adults (compare Figure A4.29 and Figure A4.35). As the population growth rate increased, the maximum reproductive value increased and the distribution of values flattened, illustrating that all age classes were generally contributing equally to future generations in this circumstance.

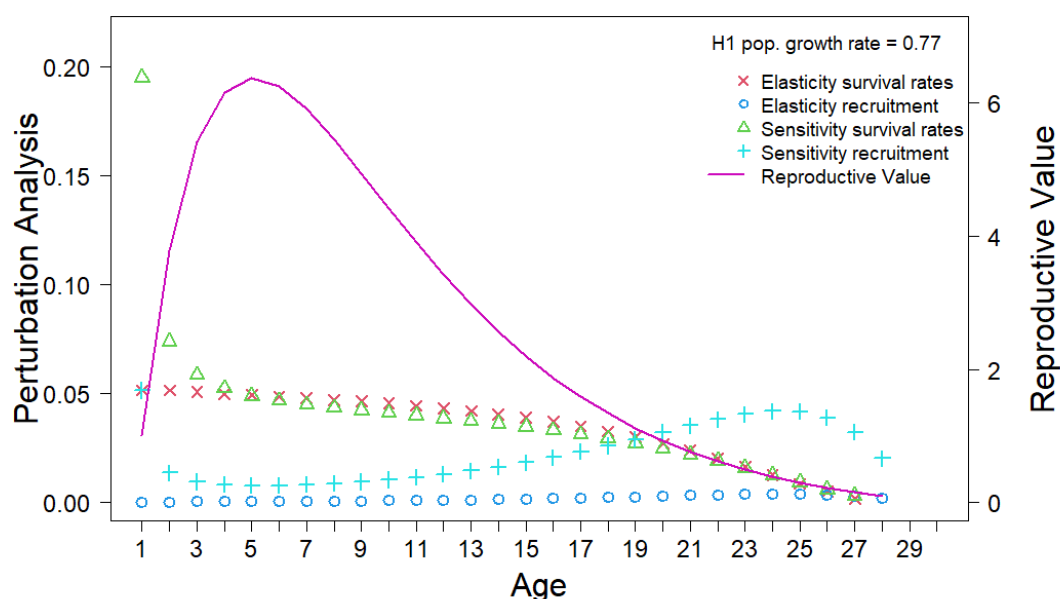


Figure A4.25. Habitat 1 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 0.77.

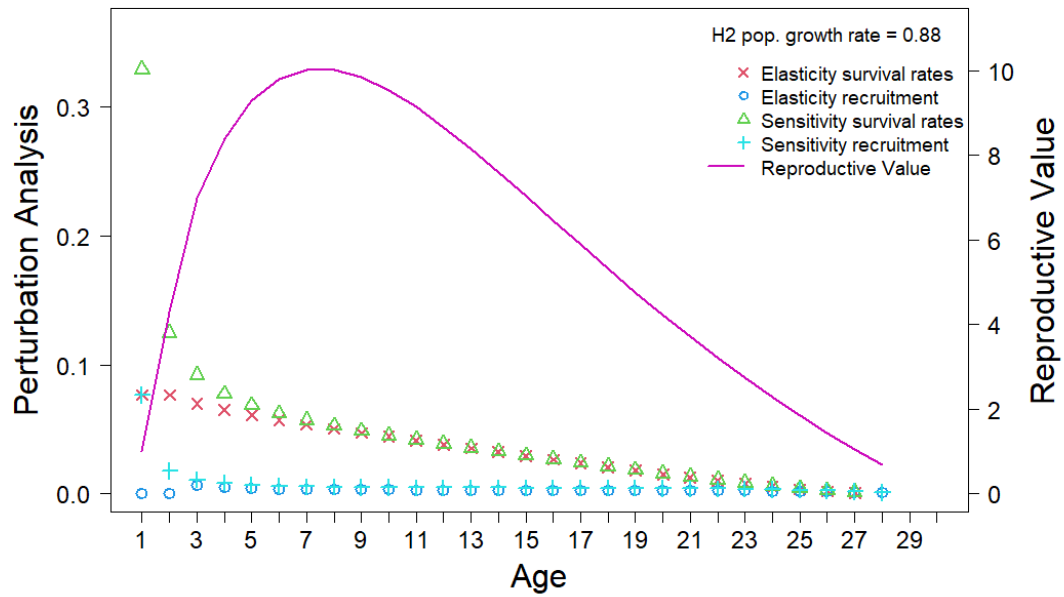


Figure A4.26. Habitat 2 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 0.88. See Table A2.1 and Table A3.1 for descriptions of the habitats and parameterisation.

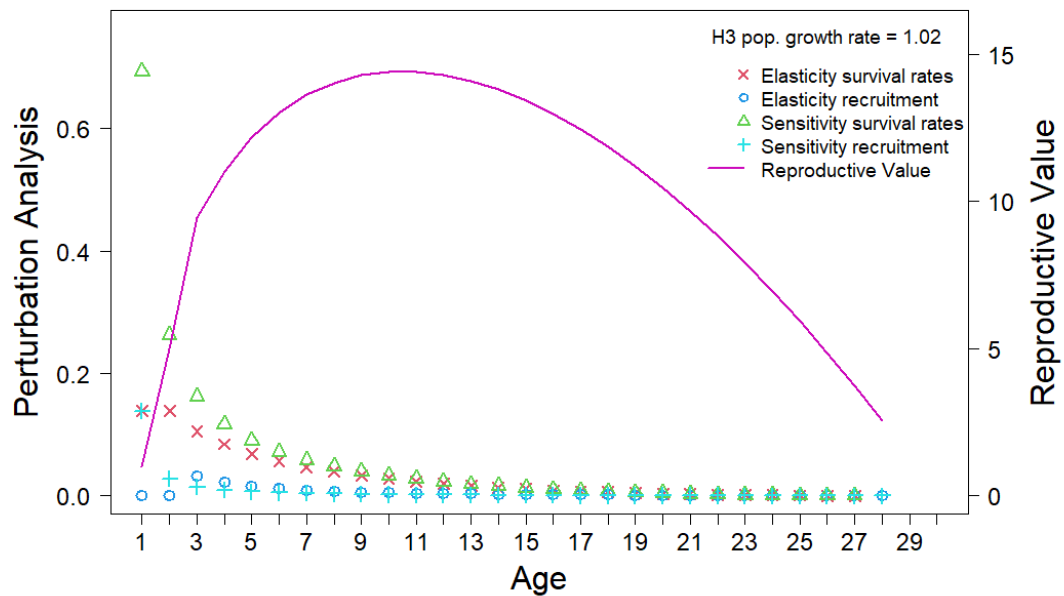


Figure A4.27. Habitat 3 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 1.02. See Table A2.1 and Table A3.1 for descriptions of the habitats and parameterisation.

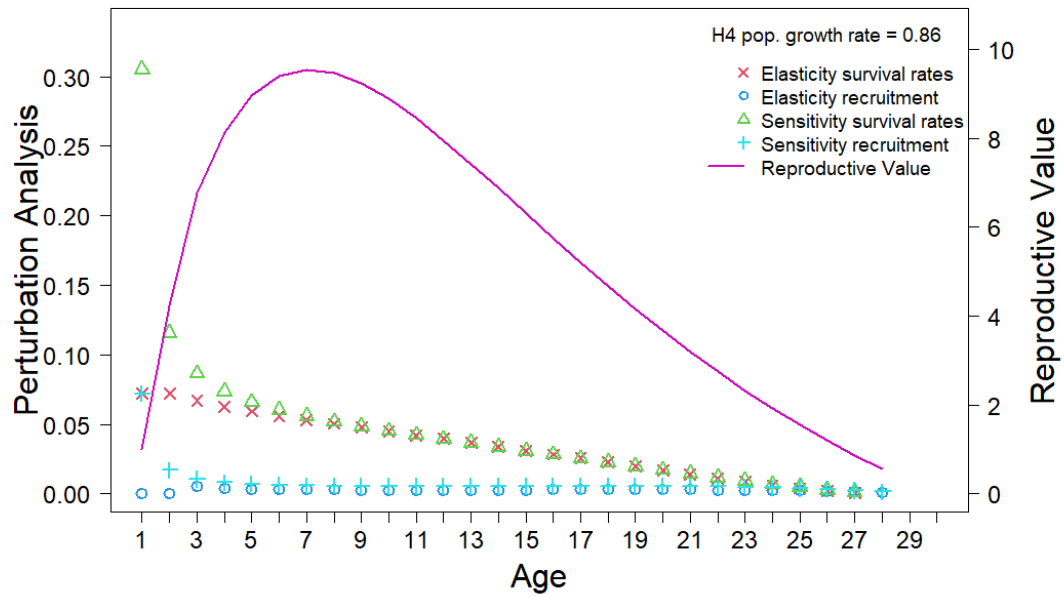


Figure A4.28. Habitat 4 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 0.86. See Table A2.1 and Table A3.1 for descriptions of the habitats and parameterisation.

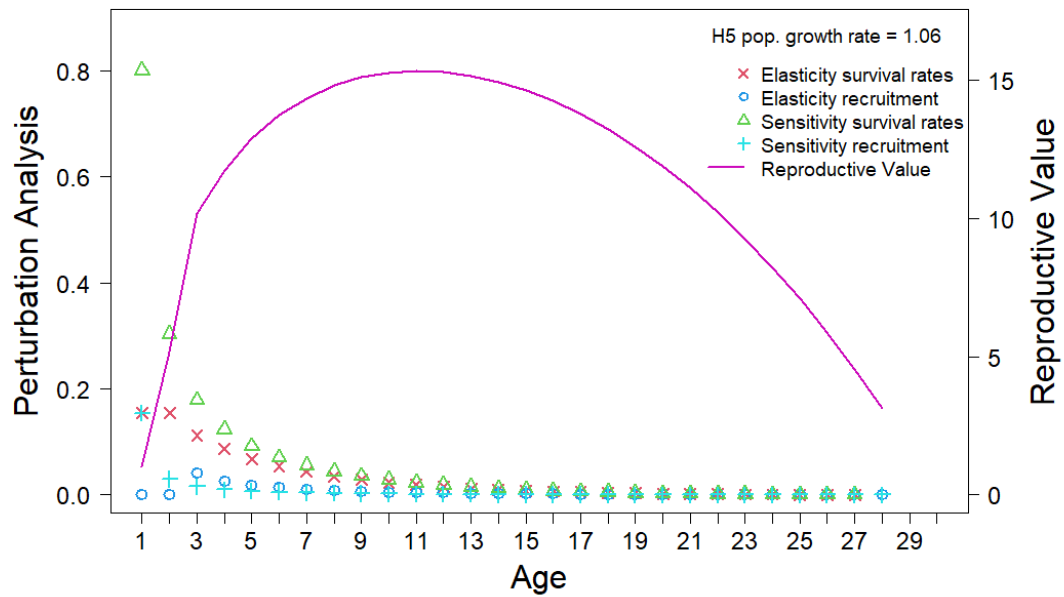


Figure A4.29. Habitat 5 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 1.06. See Table A2.1 and Table A3.1 for descriptions of the habitats and parameterisation.

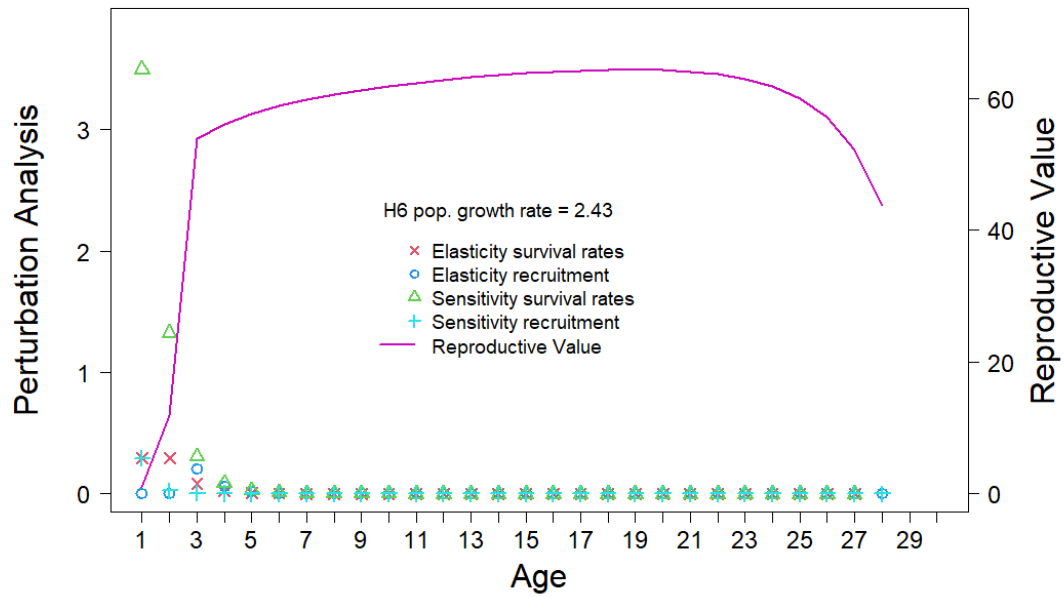


Figure A4.30. Habitat 6 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 2.43. See Table A2.1 and Table A3.1 for descriptions of the habitats and parameterisation.

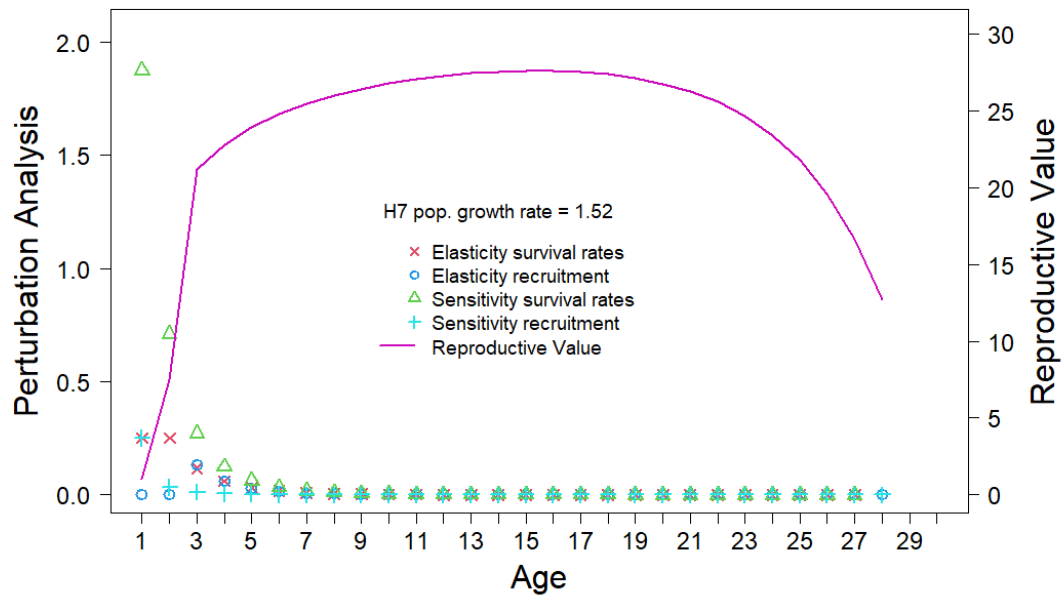


Figure A4.31. Habitat 7 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 1.52. See Table A2.1 and Table A3.1 for descriptions of the habitats and parameterisation.

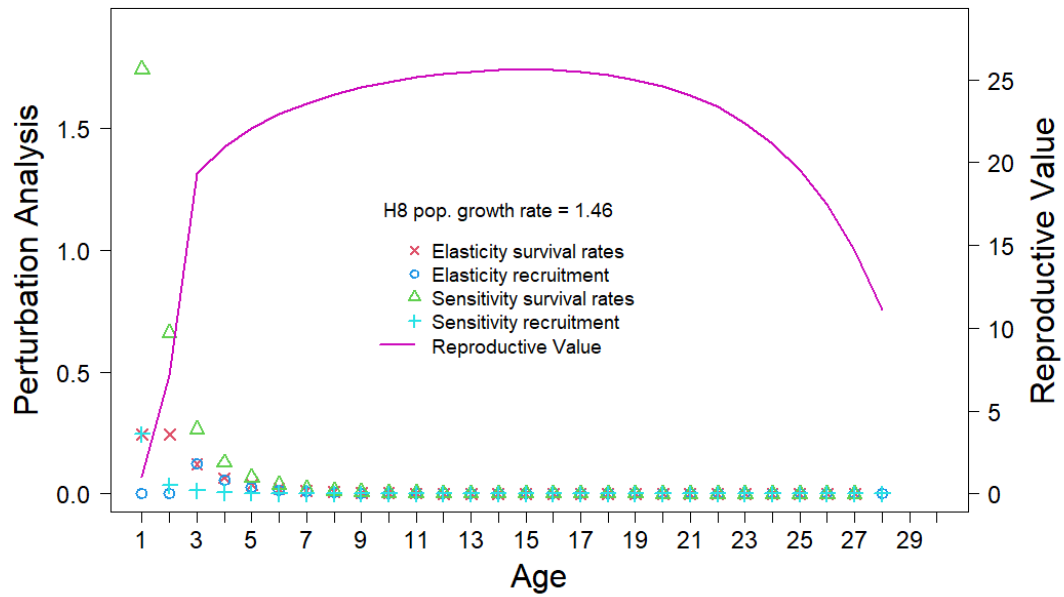


Figure A4.32. Habitat 8 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 1.46. See Table A2.1 and Table A3.1 for descriptions of the habitats and parameterisation.

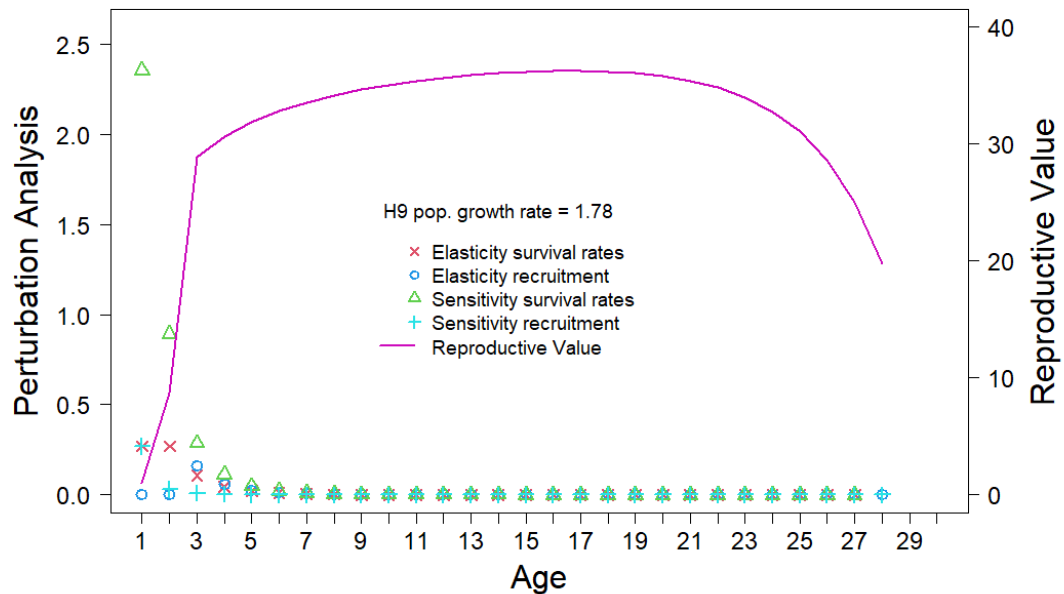


Figure A4.33. Habitat 9 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 1.78. See Table A2.1 and Table A3.1 for descriptions of the habitats and parameterisation.

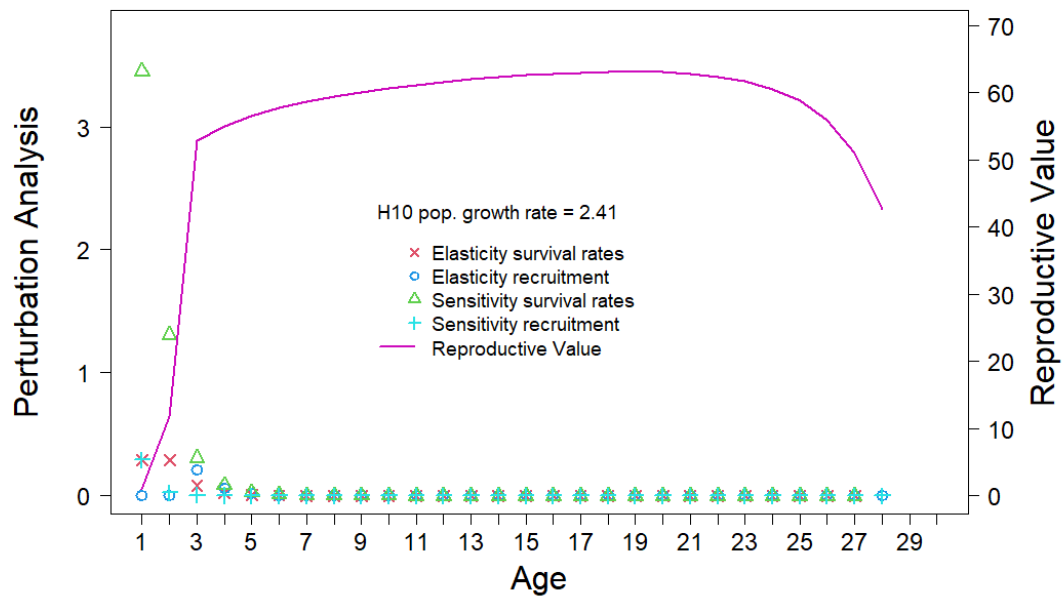


Figure A4.34. Habitat 10 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 2.41. See Table A2.1 and Table A3.1 for descriptions of the habitats and parameterisation.

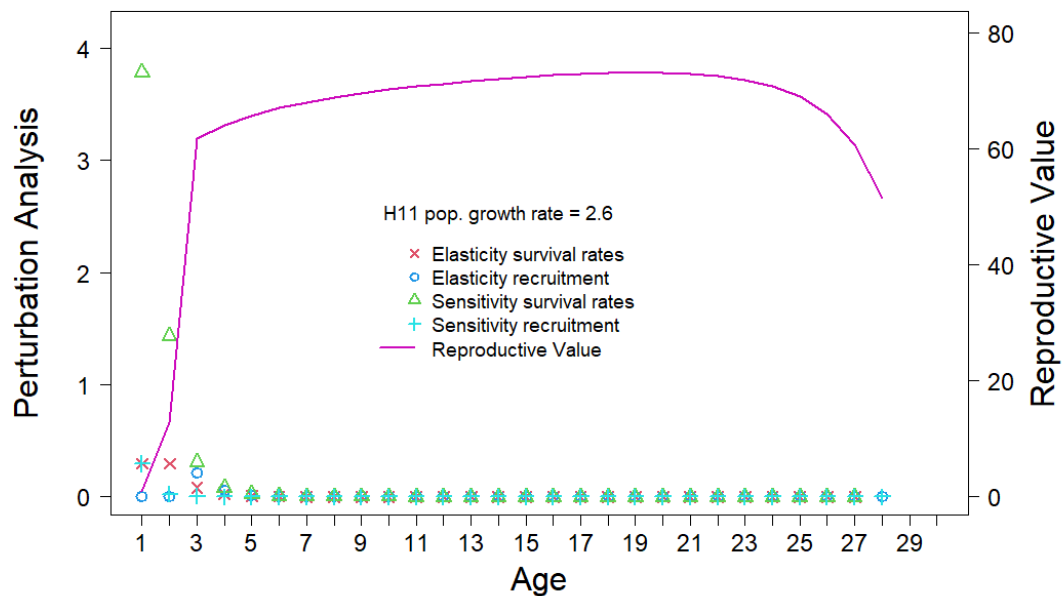


Figure A4.35. Habitat 11 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 2.6. See Table A2.1 and Table A3.1 for descriptions of the habitats and parameterisation.

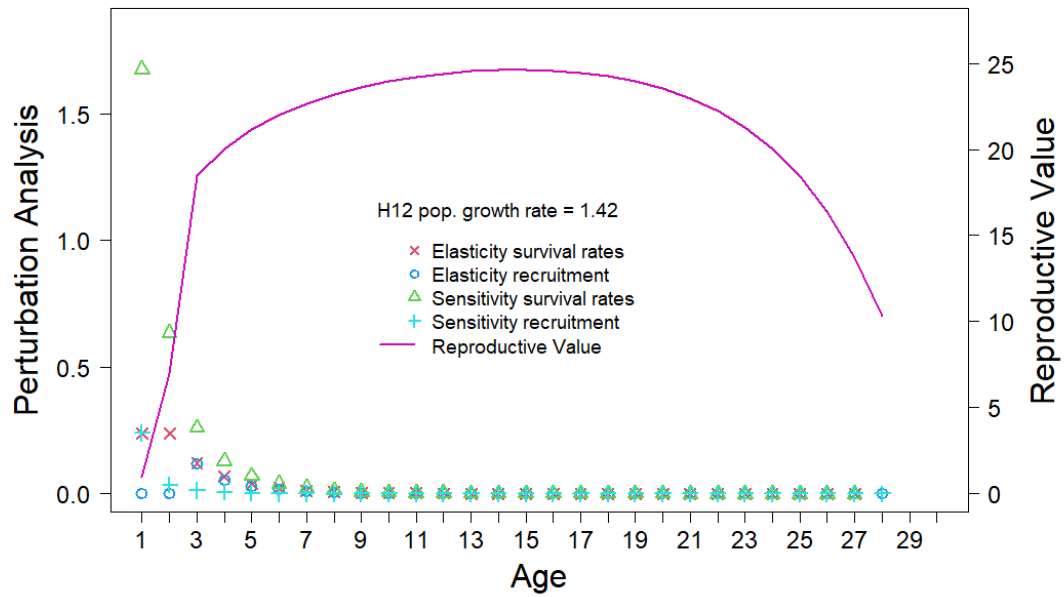


Figure A4.36. Habitat 12 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 1.42. See Table A2.1 and Table A3.1 for descriptions of the habitats and parameterisation.

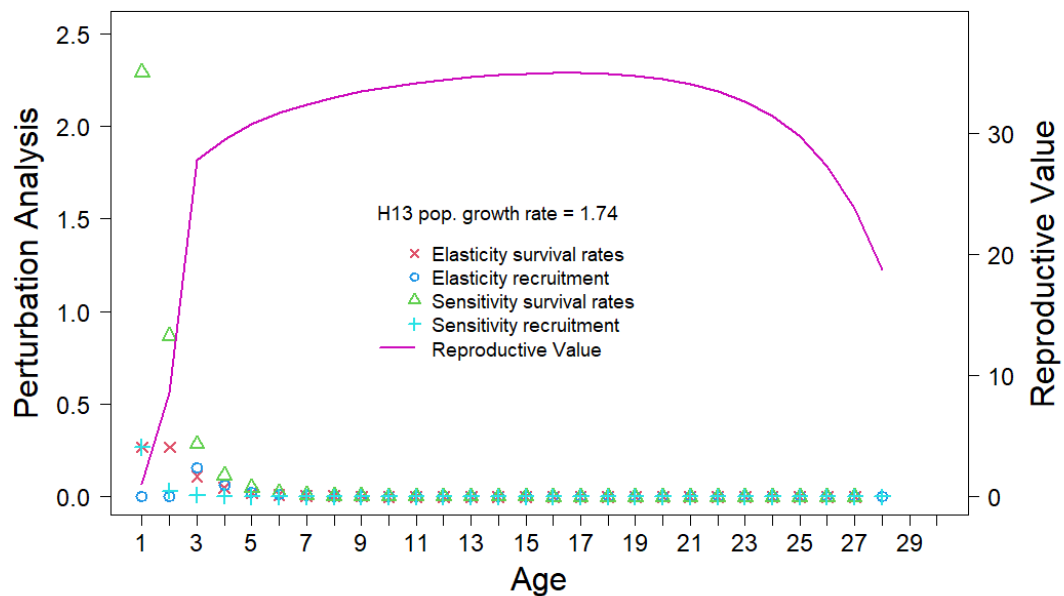


Figure A4.37. Habitat 13 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 1.74. See Table A2.1 and Table A3.1 for descriptions of the habitats and parameterisation.

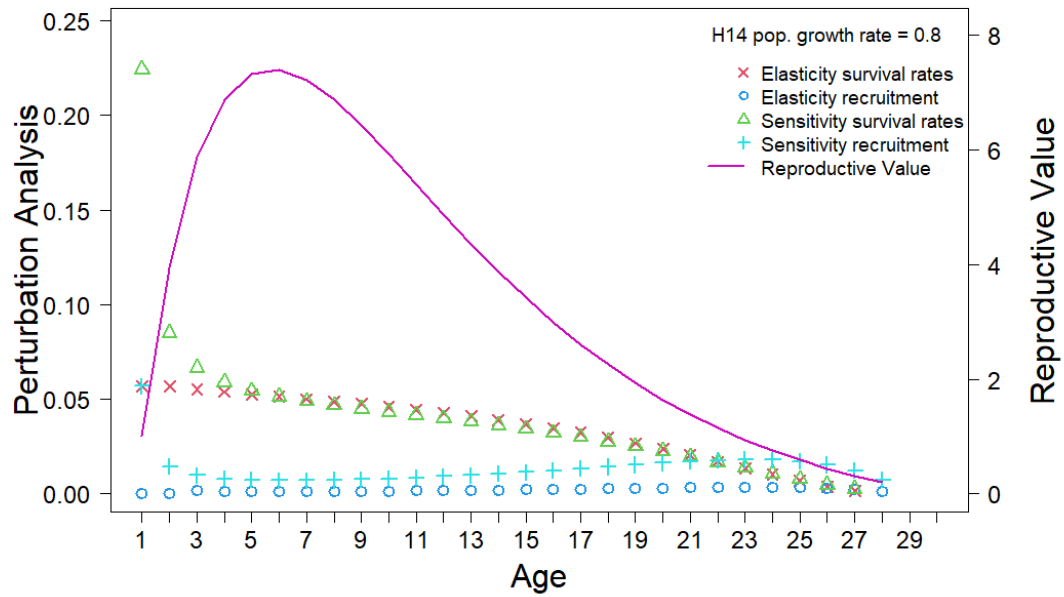


Figure A4.38. Habitat 14 elasticity analysis (sensitivity of the growth rate to proportional change in the vital rates of survival and fecundity) and reproductive values for Carp with growth rate 0.8. See Table A2.1 and Table A3.1 for descriptions of the habitats and parameterisation.

Habitat inundation inputs for populations in this study

Hume to Yarrawonga population

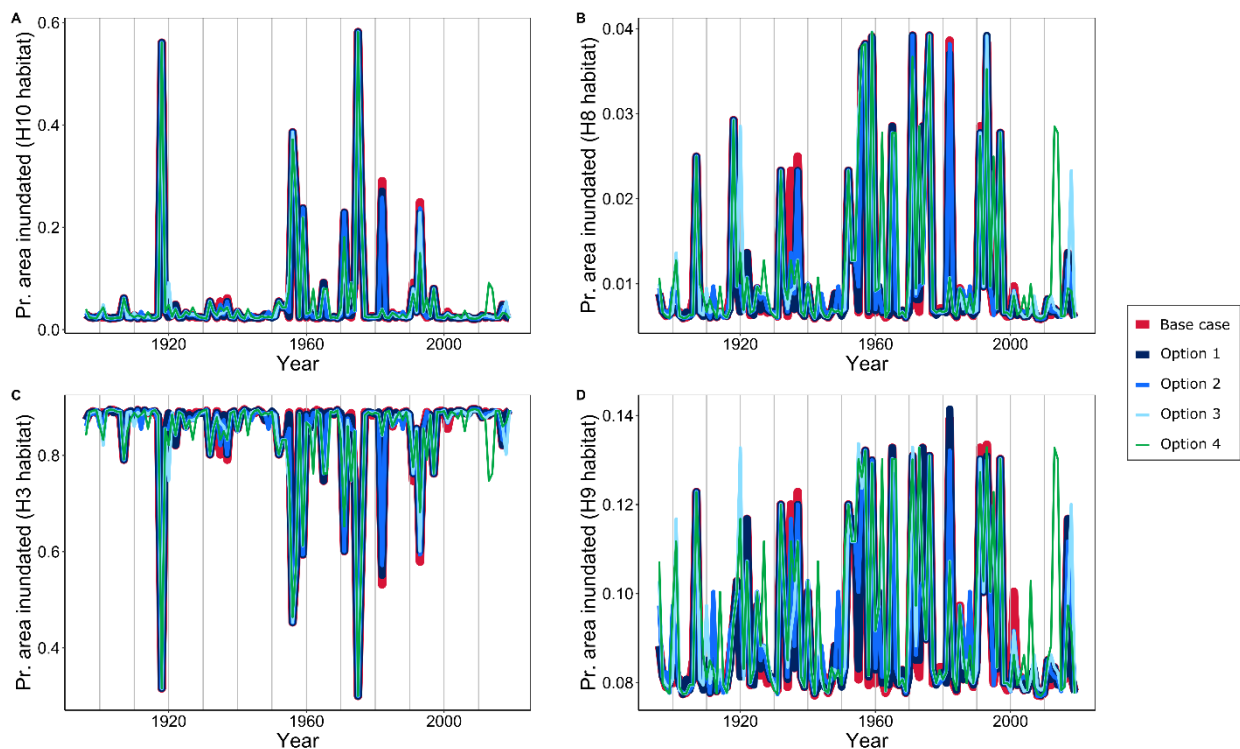


Figure A4.39. Habitat inundation estimates for the flow scenarios across the four habitats relevant for Carp life history in the Hume to Yarrawonga reach. These habitats are A: H10 habitat (natural floodplain), B: H8 habitat (wetland ephemeral), C: H3 habitat (river channel), and D: H9 habitat (wetland permanently connected). Inundation is the yearly estimate of the maximum 25-day inundation extent for each habitat, as a function of the total area of that habitat in this reach. These data form the hydrological drivers of the population model, and were generated by RiM-FIM and EW-FIM models and supplied by NSW DCCEEW.

Yarrawonga to Torrumbarry population

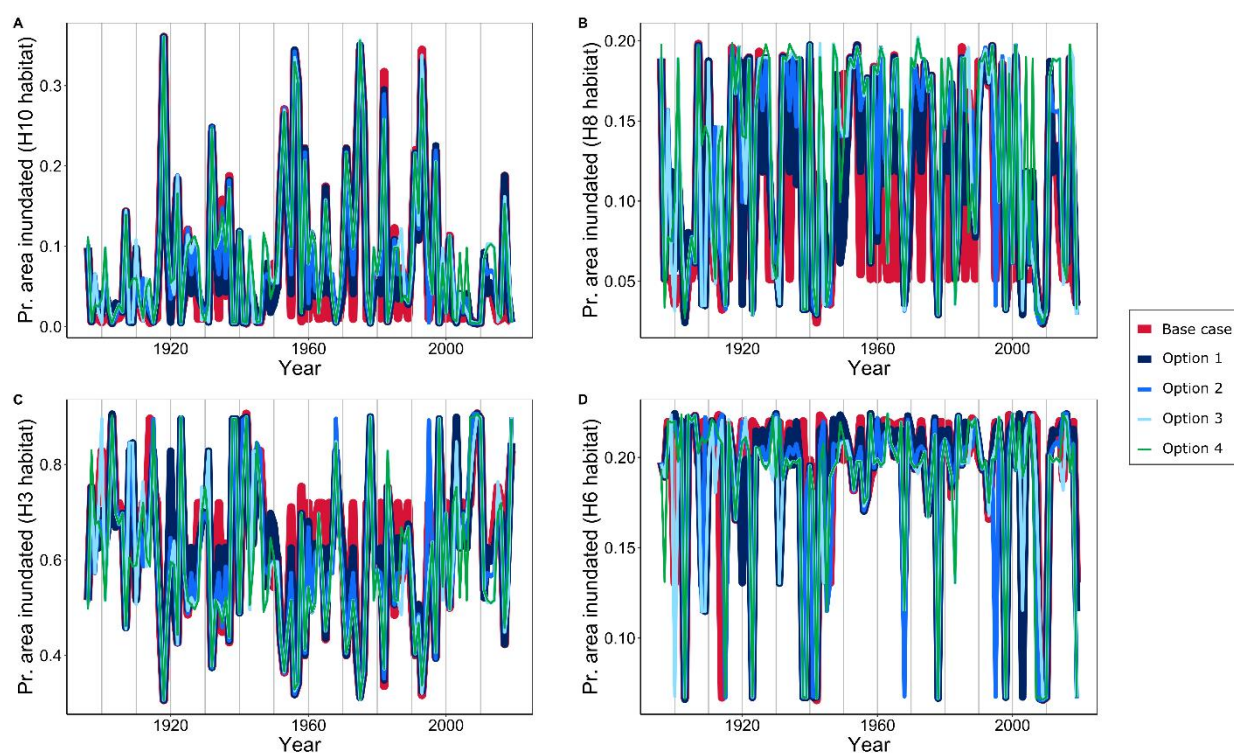


Figure A4.40. Habitat inundation estimates for the flow scenarios across the four habitats relevant for Carp life history in the Yarrawonga to Torrumbarry reach. These habitats are A: H10 habitat (natural floodplain), B: H8 habitat (wetland ephemeral), C: H3 habitat (river channel), and D: H6 habitat (river wetland). H6 habitat was used in this reach as it better reflected the habitat type that exists in this area. Inundation is the yearly estimate of the maximum 25-day inundation extent for each habitat, as a function of the total area of that habitat in this reach. These data form the hydrological drivers of the population model, and were generated by RiM-FIM and EW-FIM models and supplied by NSW DCCEEW.

Torrumbarry to Wentworth population

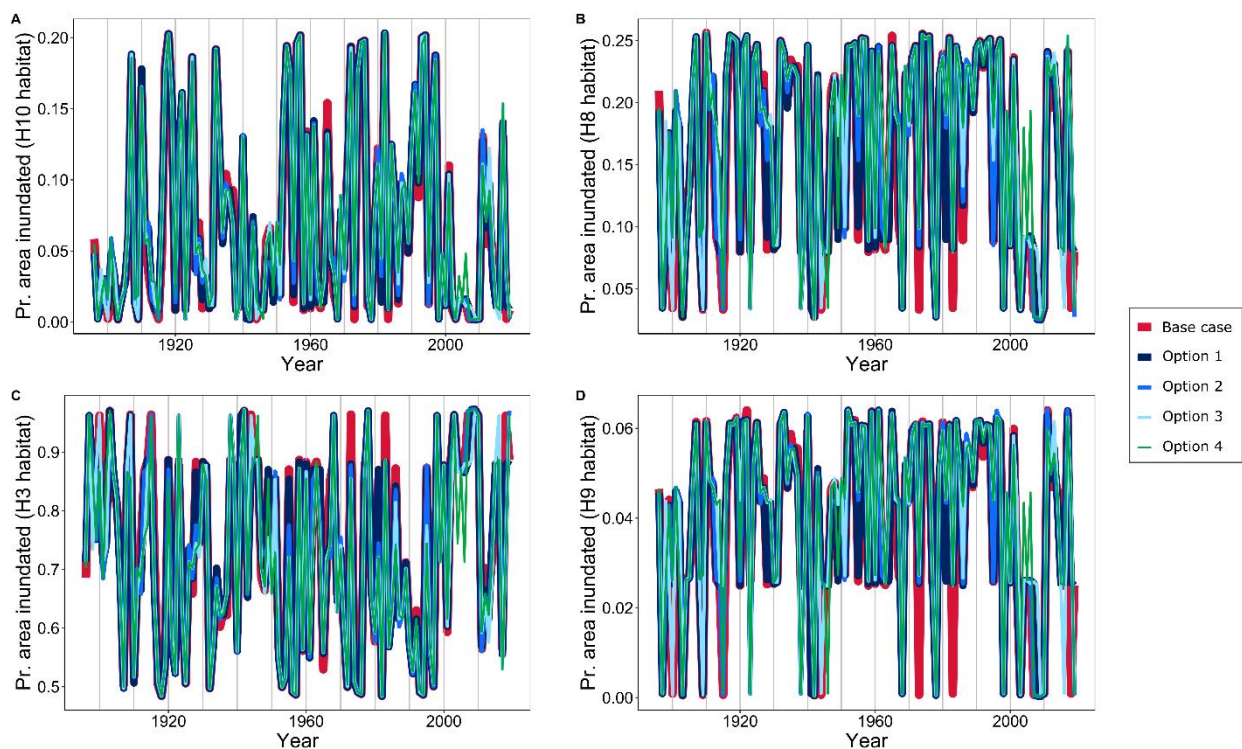


Figure A4.41. Habitat inundation estimates for the flow scenarios across the four habitats relevant for Carp life history in the Torrumbarry to Wentworth reach. These habitats are A: H10 habitat (natural floodplain), B: H8 habitat (wetland ephemeral), C: H3 habitat (river channel), and D: H9 habitat (wetland permanently connected). Inundation is the yearly estimate of the maximum 25-day inundation extent for each habitat, as a function of the total area of that habitat in this reach. These data form the hydrological drivers of the population model, and were generated by RiM-FIM and EW-FIM models and supplied by NSW DCCEEW.

Edward River population

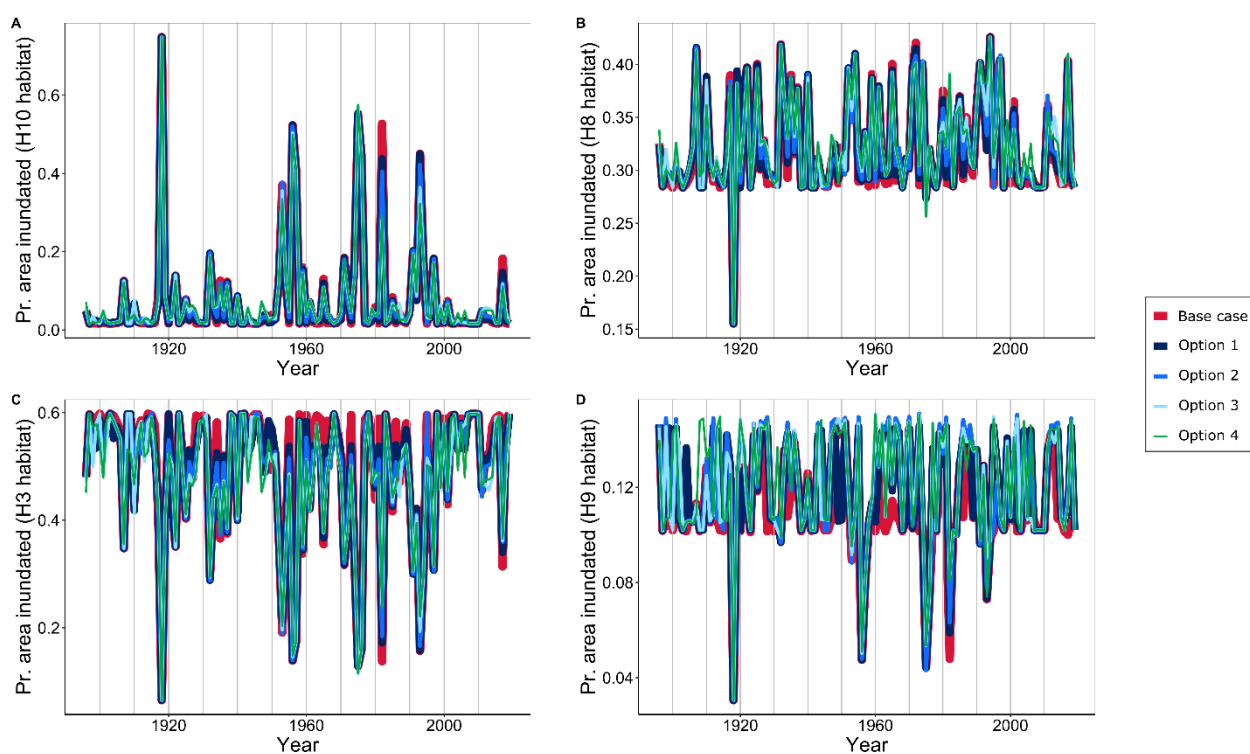


Figure A4.42. Habitat inundation estimates for the flow scenarios across the four habitats relevant for Carp life history in the Edward River. These habitats are A: H10 habitat (natural floodplain), B: H8 habitat (wetland ephemeral), C: H3 habitat (river channel) and, D: H9 habitat (wetland permanently connected). Inundation is the yearly estimate of the maximum 25-day inundation extent for each habitat, as a function of the total area of that habitat in this reach. These data form the hydrological drivers of the population model, and were generated by RiM-FIM and EW-FIM models and supplied by NSW DCCEEW.

Gundagai to Hay population

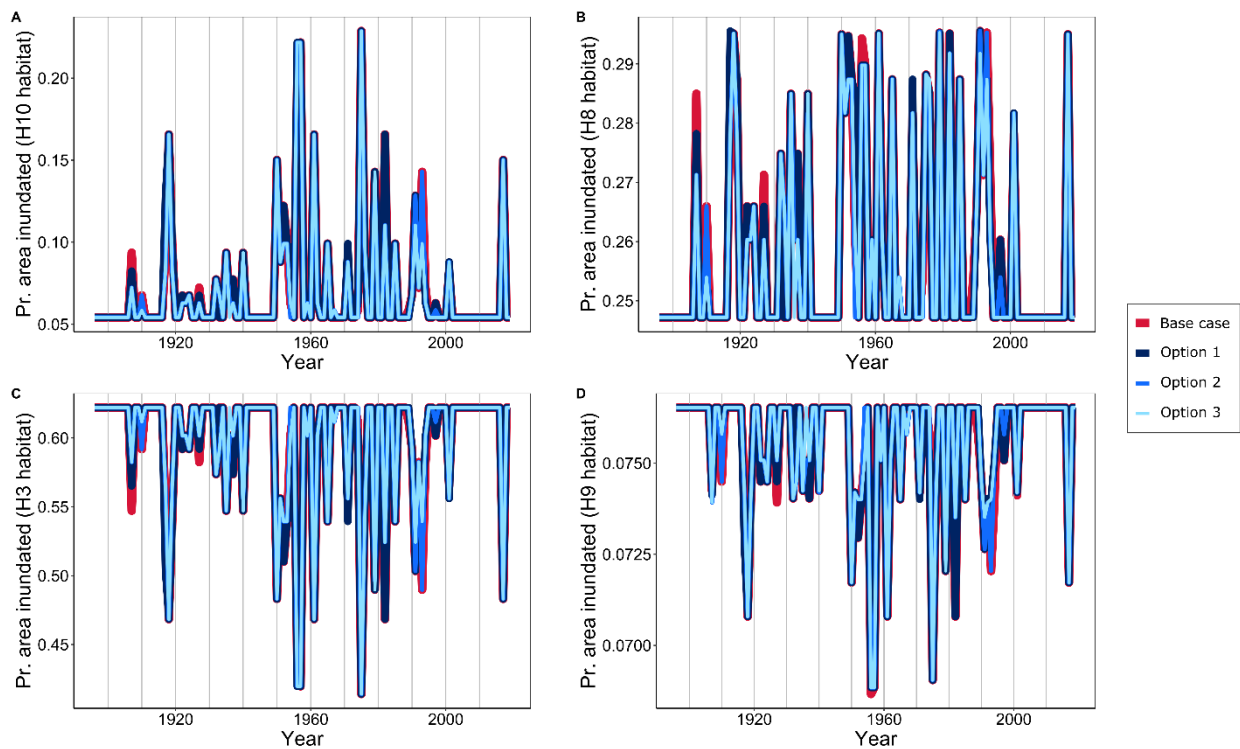


Figure A4.43. Habitat inundation estimates for the flow scenarios across the four habitats relevant for Carp life history in the Gundagai to Hay reach. These habitats are A: H10 habitat (natural floodplain), B: H8 habitat (wetland ephemeral), C: H3 habitat (river channel), and D: H9 habitat (wetland permanently connected). Inundation is the yearly estimate of the maximum 25-day inundation extent for each habitat, as a function of the total area of that habitat in this reach. These data form the hydrological drivers of the population model, and were generated by RiM-FIM and EW-FIM models and supplied by NSW DCCEEW.

Hay to Balranald population

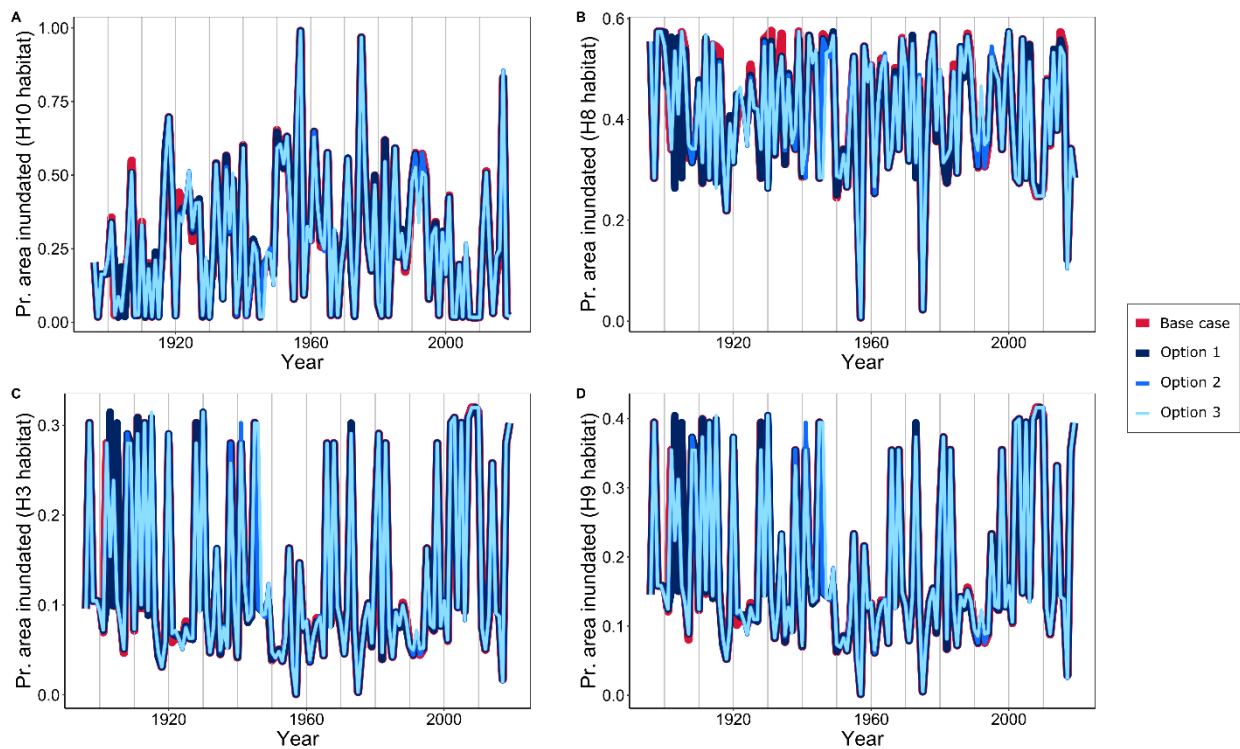


Figure A4.44. Habitat inundation estimates for the flow scenarios across the four habitats relevant for Carp life history in the Hay to Balranald reach. These habitats are A: H10 habitat (natural floodplain), B: H8 habitat (wetland ephemeral), C: H3 habitat (river channel), and D: H9 habitat (wetland permanently connected). Inundation is the yearly estimate of the maximum 25-day inundation extent for each habitat, as a function of the total area of that habitat in this reach. These data form the hydrological drivers of the population model, and were generated by RiM-FIM and EW-FIM models and supplied by NSW DCCEEW.

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