Fish population models: Sensitivity to key life history characteristics in the Murray cod and golden perch population models

Commonwealth Environmental Water Holder (CEWH): Monitoring, Evaluation and Research Program

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Acknowledgement of Country

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About Flow-MER

The Flow-MER Basin-scale Project is led by CSIRO in partnership with the University of Canberra, and collaborating with Charles Sturt University, Deakin University, University of New England, South Australian Research and Development Institute, Arthur Rylah Institute, NSW Department of Primary Industry, Australian River Restoration Centre, Brooks Ecology & Technology and Alluvium. The Program delivers to the Commonwealth Environmental Water Holder, Department of Climate Change, Energy, the Environment and Water. The authors thank all partners and project staff for their support and interest in the work reported herein.

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Document history

Version	Note
14 August 2024	Draft submitted to Flow-MER Basin-scale team (CSIRO)
19 August 2024	Review period, including report updating to address accessibility requirements
23 September 2024	Report delivered to CEWH

Cover photograph

Murray cod and golden perch (Arthur Rylah Institute)

Summary

Improvement in native fish populations is identified as a key target in the Commonwealth's (Murray–Darling) *Basin Plan* 2012 (Basin Plan). However, adaptive management of fish populations at Basin-scale is challenging due to the broad distributions and connectedness of many fish species across multiple rivers or, in some cases, across the entire Basin.

Basin-scale meta-population models for golden perch (*Macquaria ambigua*) and bony herring (*Nematalosa erebi)* and area-scale (i.e. Flow-MER Selected Areas) models for Murray cod (*Maccullochella peelii*) were developed in the Flow-MER Research Theme (project F1: Fish population models). The ultimate purpose of these models is to inform adaptive management of environmental water deliveries targeting native fish populations in the Basin (Todd et al. 2022a). This previous research program provided several recommendations, including closer integration of findings from the Flow-MER Research Theme (project F2: Fish movement), consideration of potential climate change impacts, greater consideration of processes relevant to the northern Basin, and detailed sensitivity analysis to determine the relative influence of different processes and sources of uncertainty on model projections. Incorporation of updated movement rules and climate change scenarios was completed in the previous reporting round (Todd et al. 2023).

Here, we present updates to the northern Basin component of the golden perch population model and a series of sensitivity analyses focused on the Murray cod and golden perch population models.

Research aims

- Include low-flow thresholds in the northern Basin component of the golden perch population model
- Assess the sensitivity of the Murray cod and golden perch population models to variation or uncertainty in key underlying processes.

The key processes identified for Murray cod were survival of eggs, larvae, and first- and second-stage fingerlings, while the key processes identified for golden perch were movement (of adults and juveniles combined), larval drift, and spawning cues. The project complements earlier studies from the Flow-MER Research Theme (Thiem et al. 2022, Todd et al. 2022a, 2023) and guides the future development of Basin-scale population models and their application to the adaptive management of environmental water.

Methods

We used previously developed stochastic population models for Murray cod and golden perch (Todd et al. 2022a; Todd et al. 2023). These models characterise the ecology of each species, Murray cod at Selected Areas and golden perch across major reaches in the Basin (including inter-reach movements).

For Murray cod, we assessed the sensitivity of modelled population trajectories in each Selected Area to variation in several key processes (egg, larvae, and fingerling survival), each of which is associated with a different set of flow components. We sequentially fixed each process (i.e. removed the influence of the flow components relevant to a single life stage) and projected population outcomes under observed and counterfactual flows (i.e. flows without Commonwealth Environmental Water [CEW]).

For golden perch, we expanded the model construct to include a new low-flow mechanism, which allowed us to assess low-flow thresholds and the contributions of environmental water to meeting these thresholds in the northern Basin. In addition, we assessed the sensitivity of Basin-scale population outcomes to variation in the following processes: upstream:downstream movement ratios, thresholds for flow-cued spawning, and larval drift responses to flow.

Results

Modelled Murray cod population trajectories were most sensitive to variation in the (in-channel) flow components associated with egg and larval survival and less sensitive to variation in the flow components associated with fingerling survival. In all Selected Areas, including the effects of relevant flow components had a positive influence on larval survival, which suggests that these flow components (represented by low flow variability from Oct–Dec) were generally conducive to higher larval survival. By contrast, including the effects

of relevant flow components had a negative influence on egg survival, which suggests that the observed variation in these flow components (antecedent flows and Oct–Dec water temperatures) tended to reduce Murray cod egg survival relative to a scenario in which these components were held constant at their average value.

The golden perch metapopulation generated varied and complex responses under the different sensitivity scenarios. Overall, the model exhibited low-to-moderate sensitivity to changes in the model rules. Populations in the southern Basin were generally more sensitive to changes in the rules determining spawning and larval drift, whereas populations in the northern Basin were more sensitive to changes in the rules determining juvenile and adult movement rates and the newly incorporated rules representing low-flow impacts. For both Murray cod and golden perch, the sensitivity of model outputs to changes in underlying parameters was consistent in scenarios with and without CEW.

Conclusions and implications

A key aim of sensitivity analysis is to identify specific processes or life stages for which variation or uncertainty in parameters has a disproportionate impact on modelled outcomes.

> We identified egg and larval survival as key determinants of Murray cod population outcomes, with uncertainty in these parameters and their associations with flows likely to have large impacts on modelled population dynamics.

> Similarly, the golden perch metapopulation model was sensitive to all tested processes, but the relative influence of these processes differed between the northern and southern Basin.

Importantly, our study revealed that uncertainty in processes occurring in one region has the potential to affect population outcomes elsewhere in the Basin, which highlights the Basin-scale nature of golden perch populations (and our metapopulation model).

> Although our analysis identified some differences in population outcomes in scenarios with and without CEW, the sensitivity of model outcomes to key parameters did not markedly affect the predicted outcomes of CEW for either species.

> This finding suggests that the current counterfactual approach (i.e. estimating population outcomes under scenarios with and without CEW) is robust to uncertainty in model assumptions.

This finding provides confidence that population models, including the Basin-scale golden perch model, are appropriate tools to assess the contributions of CEW to improving native fish populations in the Basin.

Recommendations

Based on our findings, we provide the following recommendations:

1 Incorporate population models in the Flow-MER fish evaluation

Embedding population models in evaluations would support a quantitative assessment of population outcomes with and without CEW and would provide greater opportunities to implement and validate the population models. In particular, and as demonstrated in earlier outputs of the Flow-MER Research Theme (project F1: Fish population models), the Basin-scale golden perch model provides a unique opportunity to assess Basin-scale outcomes of CEW (including outside of Selected Areas).

2 Develop targeted research projects to strengthen understanding of the early life history of Murray cod

High sensitivity of modelled Murray cod population outcomes to variation in the flow components associated with egg and larval survival indicates a need to develop targeted research projects to strengthen understanding of the early life history of Murray cod. Key flow components identified in the sensitivity analysis include flow variability and water temperatures from Oct–Dec and antecedent flow conditions. Current conceptual understanding of these flow components indicates that they influence Murray cod via their impacts on hydraulic conditions, instream productivity, and physical habitat availability during and immediately following spawning. Improving the availability of data on these factors and knowledge of their links to Murray cod population dynamics will require greater collaboration among Flow-MER Themes.

3 Complement the Basin-scale golden perch model with empirical research examining differences in golden perch population dynamics across the Basin

High sensitivity of modelled golden perch population outcomes to early life stages (eggs and larvae) in the southern Basin and juvenile and adult stages in the northern Basin suggests a need to complement the Basin-scale golden perch model with empirical research examining differences in golden perch population dynamics across the Basin. Empirical research has previously been used to refine and validate the golden perch model in the southern Basin (with a particular focus on movement rules among populations). Further empirical work could address remaining uncertainties around egg and larval drift, as well as movement rules and low-flow impacts in the northern Basin (see Recommendation 4). Empirical data would additionally support efforts to evaluate Basin-scale outcomes of CEW independently of the population model.

4 Quantify low-flow impacts on golden perch survival to refine low-flow thresholds for golden perch

The model currently incorporates flow recommendations for the northern Basin and reduces survival of all age classes when the low-flow threshold is not met (i.e. when flows are too low). However, it is likely that flows affect golden perch populations at levels above this threshold. In addition, the duration of low flows is likely to interact with the magnitude of these flows, and the impacts of different magnitude-duration combinations on golden perch populations is not currently well understood. Clarification of the processes underpinning low-flow thresholds in the northern Basin is also required. This includes determining fundamental thresholds below which fish survival is reduced, as well as determining the contributions of different water deliveries (including but not limited to environmental water) to exceeding the low-flow thresholds in the northern Basin.

Murray cod
Photo credit: Arthur Rylah Institute

Golden perch
Photo credit: Arthur Rylah Institute

Overview of Flow-MER

The Commonwealth Environmental Water Holder (CEWH) invests in monitoring, evaluation and research activities delivered through an integrated program called the Monitoring, Evaluation and Research (Flow-MER) Program. This program builds on work undertaken through the Long-Term Intervention Monitoring (LTIM) and Environmental Water Knowledge and Research (EWKR) Projects (2014–2019) to monitor and evaluate the contribution of Commonwealth water for the environment to environmental outcomes in the Murray–Darling Basin. The Flow-MER Program:

- monitors and evaluates ecological responses to Commonwealth environmental water in 7 Selected Areas and at basin-scale using established metrics and methodologies
- undertakes best-practice science in 7 Selected Areas and at basin-scale to research ecological processes and thus improve capacity to understand and predict how ecosystems respond to water management
- demonstrates outcomes from Commonwealth environmental water and documents these via a regular reporting schedule and engagement and extension activities
- facilitates a regular, timely and effective transfer of relevant knowledge to meet the adaptive management information requirements of Commonwealth environmental water decision-makers.

Up-to-date Flow-MER Program information on and outcomes are available from the Flow-MER website.

Flow-MER research

The Flow-MER Program is the primary means by which the Science Program of the CEWH undertakes research to deliver improved methods and a richer evaluation of environmental outcomes from Commonwealth environmental water. Flow-MER Research aims to improve basin-scale understanding of the contribution of Commonwealth environmental water within and outside of Selected Areas, develop new approaches to evaluating outcomes, support adaptive management and develop a richer understanding of ecological processes and responses to Commonwealth environmental water.

The Research Plan has evolved from the LTIM and builds on the EWKR research priorities together with a large body of previous work, resulting in 13 research projects: Flow-ecology (BW2), Condition response (E2), Non-woody plants (V1), Woody plants (V2), Fish population models (F1), Fish movement (F2), Waterbirds (E1), Refugia (BW1), Scaling and condition (E3), Bioenergetics (BW3), Visualisation (CC1), Modelling (CC2) and Indigenous engagement (CC3).

About this report

This report has been prepared by the Arthur Rylah Institute of the Victorian Department of Energy, Environment and Climate Action (DECCLA) and is the deliverable from the 2023–24 F1 Fish population modelling research project. Queries on this report can be directed to Arthur Rylah Institute for Environmental Research, Department of Energy, Environment and Climate Action, PO Box 137 Heidelberg, VIC 3084. Phone (03) 9450 8600, website www.ari.vic.gov.au.

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1 Introduction

Environmental water (including Commonwealth environmental water [CEW]) is a key action for the protection and restoration of water-dependent ecosystems in the Murray Darling Basin (the Basin). The Commonwealth's (Murray–Darling) *Basin Plan 2012* (Basin Plan) identifies a series of targets to measure progress towards high-level environmental objectives, and these targets include improvements in population outcomes for native fish. However, it is challenging to distinguish the benefits of delivered water from the effects of natural flows, especially at ecologically relevant scales (which often extend beyond sites, rivers, and state borders). The Commonwealth Environmental Water Holder's Basin-scale Monitoring, Evaluation and Research program (Flow-MER) was designed to measure the contribution of Commonwealth Environmental Water (CEW) to native fish populations at Selected Areas across the Basin. A key challenge for this Program has been the evaluation of Basin-scale environmental outcomes, which, ideally, requires information on outcomes outside of Selected Areas, as well as knowledge of interactions or connections between Selected Areas (or other key sites in the Basin).

We previously developed a series of population models under Flow-MER Research Theme (project F1: Fish population models). Specifically, we developed Basin-scale metapopulation models for golden perch (*Macquaria ambigua*) and bony herring (*Nematalosa erebi*) and Area-scale models for Murray cod (*Maccullochella peelii*). All 3 models use best-available knowledge of the links between river conditions and key life history characteristics (e.g. survival and reproduction) to predict fish population outcomes under a range of flow, temperature, and management scenarios, but we recognise that knowledge at the time of model development (as sourced from published literature and expert opinion workshops) may be incomplete and considerable uncertainty remains for many of these flow ecology relationships (Todd et al. 2022a). The golden perch and bony herring models explicitly include flow-dependent movement among 14 populations spanning the Basin. The Murray cod model was specified separately for each Selected Area given Murray cod's low propensity for long-distance movements. Importantly, these models were derived from fundamental ecological processes, current understanding of which can be tested, modified, and updated as new information becomes available.

Population models, and Basin-scale metapopulation models in particular, provide a unique tool to inform the adaptive management of Basin-scale environmental water deliveries targeting native fish populations (Todd et al. 2022a). In earlier outputs from the Flow-MER Fish Research Theme, population models were used to assess how fish populations respond to managed flows, including an evaluation of Basin-scale outcomes under historical scenarios with and without CEW (i.e. a counterfactual approach). This previous research program provided several recommendations, including closer integration of findings from the Flow-MER Fish Research Theme (project F2: Fish movement), consideration of potential climate change impacts, greater consideration of processes relevant to the northern Basin, and detailed sensitivity analysis to determine the relative influence of different processes and sources of uncertainty on model projections (Todd et al. 2022a). Incorporation of updated movement rules and climate change scenarios were completed in the previous reporting round (Todd et al. 2023). Here, we present updates to the northern Basin component of the golden perch population model and a series of sensitivity analyses focused on the Murray cod and golden perch population models.

1.1 Aims

The overarching aim of this project was to add low-flow thresholds in the northern Basin to the golden perch metapopulation model and assess the sensitivity of population model outputs to variation or uncertainty in key underlying processes. We focused here on the Area-scale Murray cod population model for all areas and the Basin-scale golden perch metapopulation model. The key processes identified for Murray cod were survival of eggs, larvae, and first- and second-stage fingerlings, each of which is associated with a different set of flow components. The key processes identified for golden perch were movement (of adults and juveniles combined), larval drift, spawning cues, and newly incorporated low-flow thresholds in the Northern Basin.

The project has the following specific aims:

- Extend the golden perch metapopulation model to include a low-flow mechanism that captures the impacts of flow conditions below the low-flow thresholds specified in water management plans for the northern Basin.
- Assess the sensitivity of modelled Murray cod population trajectories to variation or uncertainty in flow-ecology links specific to early life stages (eggs, larvae, and fingerlings).
- Assess the sensitivity of modelled golden perch metapopulation trajectories to variation or uncertainty in flow-cued movement, larval drift, and spawning.
- Examine how model sensitivity (addressed in Aims 1–3) affects modelled impacts of CEW on native fish populations.

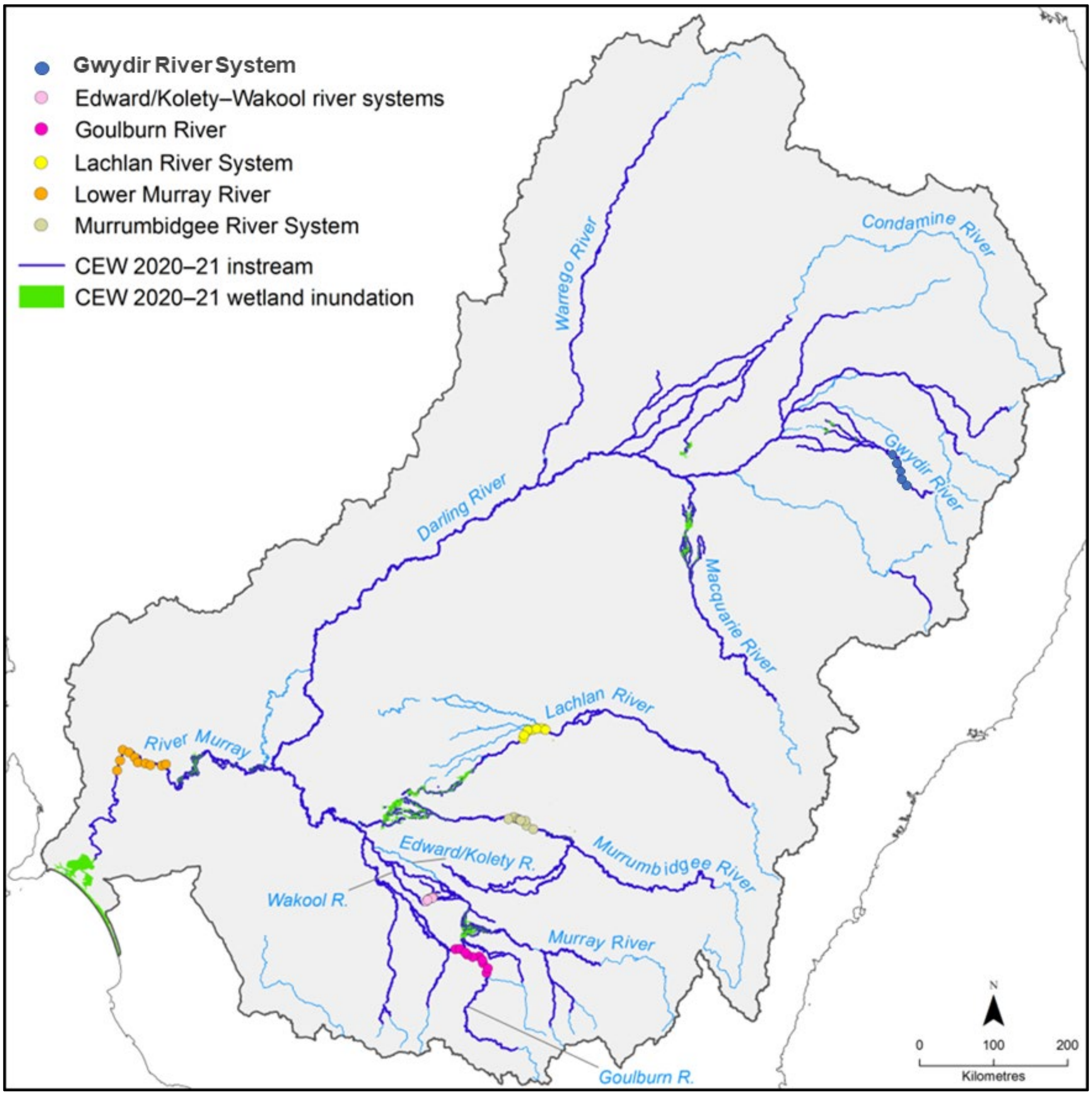
This project complements earlier studies from the Flow-MER Research Theme (Thiem et al. 2022, Todd et al. 2022a, 2023) and informs the future development of Basin-scale population models and their application to the evaluation and adaptive management of environmental water.

2 Methods

2.1 Population models

The models used in this project were developed in an earlier project to inform the delivery of Commonwealth environmental water (CEW) in the Murray–Darling Basin (the Basin), with native fish being a key target of environmental water deliveries (Todd et al. 2022a). As part of this earlier project, population models were developed for Murray cod in 6 (of the 7) Selected Areas (Figure 2.1) and a Basin-scale metapopulation model was developed for golden perch. These models were revised to include updated movement rules (based on the findings of Basin-scale Flow-MER Fish Research Theme, Project F2: Fish movement) and to assess the potential impacts of future climate change (Todd et al. 2023). Details of model development are provided in Todd et al. (2022a, 2022b) and a mathematical description of the models is included in Appendix A. Here, we focus primarily on describing the changes to the models required to address Aims 1–4, set out in Chapter 1.

Figure 2.1 Map of the Basin showing the 6 Flow-MER Selected Areas in which customised individual Murray cod population models were constructed to evaluate the influence of environmental water on population dynamics



2.1.1 Murray cod

The Murray cod population model is a stage/age matrix construct (Todd and Koehn 2007; Koehn and Todd 2012). The model summarises the life history of Murray cod by explicitly representing 50 age classes (Koehn and Todd 2012), with Murray cod assumed to become sexually mature at 5 years of age and fecundity assumed to increase with age as a function of the average length of each age class (Rowland 1998a, 1998b). Murray cod are assumed to follow a 1:1 sex ratio, with the annual spawning season modelled from the beginning of October to the end of December. The model tracks female fish and the 1:1 sex ratio means that the number of males does not limit population size, with modelled population abundances doubled to convert the female population to an estimate of total population size. Further detail on the model is given in Todd et al. (2022a, 2022b, 2023).

The Murray cod population model includes variation in key early life history parameters: egg, larvae, first and second stage fingerling survival, with Area-specific associations with flows used to introduce inter-annual variation in vital rates. This construct enables projections of population trajectories under different flow scenarios (e.g. in different locations or with vs without CEW). In addition, the model can account for variation in a range of non-flow factors (e.g., stocking and habitat availability).

Initial population size of female adults was specified separately for populations in each of 6 Flow-MER Selected Areas (Figure 2.1; Gwydir River, Edward River, Goulburn River, Lachlan River, Lower Murray River, Murrumbidgee River) and the model was run for 50 time-steps as a 'burn-in' period to reduce the influence of initial conditions on final model outputs, with the hydrological time series (described in Section 2.2, below) beginning after these 50 time-steps. As the model is stochastic (i.e. model parameters are drawn from probability distributions), each model run included 1000 replicates (i.e. there were 1,000 different population trajectories to characterise each scenario).

2.1.2 Golden perch

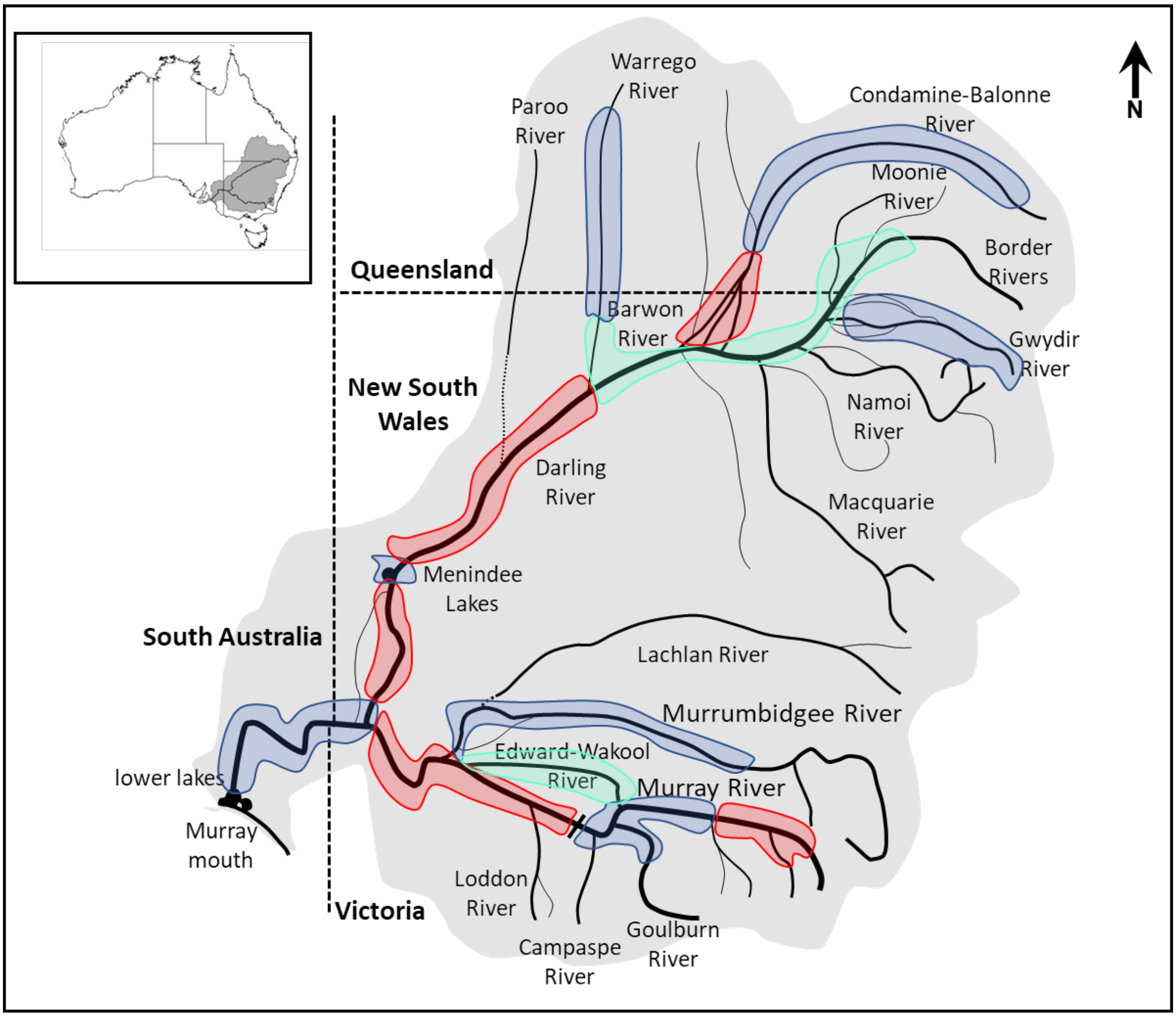
Golden perch are a wide-ranging, flow-dependent species (Zampatti et al. 2018), which necessitated the construction of a metapopulation model to capture their life history. This model included 14 populations, with a stage/age matrix model specific to each population and flow-dependent immigration and emigration between adjoining upstream and downstream populations (Figure 2.2) (Todd et al. 2022a, 2022b, 2022c, 2023). For each of the populations within the Basin metapopulation, a stage/age matrix model with four early life stages (eggs, larvae, juveniles, adults) and 30 ages was constructed to represent the life cycle of golden perch. Sexual maturity in the model occurs at 4 years of age (Mallen-Cooper and Stuart 2003), and egg production increases with age (Rowland 1996, 2005), with an assumed 1:1 sex ratio.

Inter-annual variation in metapopulation outcomes is determined by a series of rules: flow and temperature (above 17°C) determine annual spawning in each location in the southern Basin and flow alone determines spawning in the northern Basin, where temperature is not considered to be limiting; flow defines egg and larval drift from a population to its downstream neighbour; flow defines juvenile and adult movement from a population to its upstream or downstream neighbour; and flow defines larval survival via a modelled productivity relationship. The model tracks female fish, and the 1:1 sex ratio means that the number of males does not limit population size, with modelled female population abundances doubled to represent the total population. Further details on the model are given in Todd et al. (2022a, 2022b, 2023).

Initial population sizes (of female adults) were specified separately for each population, and the model was run with the hydrological time series (described in Section 2.2, below) beginning after a 50 time-steps burn-in period. As the model is stochastic (i.e., model parameters are drawn from probability distributions), each model run included 1000 replicates (i.e., there were 1000 different population trajectories to characterise each scenario).

Figure 2.2 Map of the Basin showing the 14 populations (shown as alternating blue, red and aqua polygons to distinguish adjacent populations) included in the golden perch meta-population model

Modelling was used to determine the effects of different flow scenarios on Basin-scale population outcomes. Flow scenarios influence metapopulation outcomes via their (modelled) effects on key life history characteristics (e.g., movement, spawning, drift, and low flow effects) within and between each population.



2.2 Hydrological scenarios

Flow scenarios were prepared by the Flow-MER Hydrology Theme and included observed daily flows (with CEW) at gauges across the Basin at each Selected Area from 2014–23 and modelled flows without CEW for this same period (Sengupta et al. 2024). The flow data was combined with daily temperature data for each relevant gauge (Table 2.1). This flow and temperature data were then repeated 5 times to generate 45 years of data, which allowed us to capture long-term fish population dynamics (necessary given both study species are long-lived). Flow and temperature data were used to introduce inter-annual variation into life-history processes for both modelled species (Todd et al. 2005, Michie et al. 2020; see Todd et al. 2022a for a description) and to determine population-level responses to scenarios with and without CEW contributions.

Table 2.1 List of gauges used in the golden perch metapopulation model

Fish population number	Gauge location	Gauge number
1	Lock 10 (Wentworth)	452010
2	Torrumbarry	409207
3	d/s Yarrawonga	409025
4	Doctors Point	409017
5	u/s Weir 32	425012
6	Hay	410136
7	d/s Stevens Weir	409023
8	Louth	425004
9	Mungindi	416001
10	Yarraman Bridge	418004
11	Fords Bywash	432002
12	Whyembah	42204A
13	Louden Bridge	422333A

2.3 Sensitivity analyses

2.3.1 Murray cod

The Murray cod population model uses flow characteristics to predict early life history responses via population-specific coefficients. Specifically, this construct is used to predict variation around mean survival rates of eggs, larvae, and fingerlings (two separate stages combine to produce an overall fingerling survival rate). The coefficients for each life history stage are estimated from empirical data linking observed flows to early life history responses for Murray cod in several locations across the southern Basin (Tonkin et al. 2021). Murray River coefficients (as estimated in Tonkin et al. 2021) were used for all populations in this study, which introduces an assumption that Murray cod populations operate similarly throughout the Basin. Under this construct, the number and survival rate of eggs is influenced by the maximum antecedent flow (a proxy for productivity and the condition of spawning adults) and water temperature during the spawning season, larval survival is driven by flow variability, the survival of the first stage of fingerlings is influenced by the spring flow (a proxy for productivity and food availability in the system when Murray cod reach this first fingerling stage), and survival of the second fingerling stage is determined by summer flows (Tonkin et al. 2021).

We ran a series of modelling scenarios to test the sensitivity of model outputs to flow-derived variation in survival of each life stage (eggs, larvae, and the first- and second-fingerling stages). We sequentially removed flow-derived variation from each life stage (while retaining this variation for all other life stages), which allowed us to isolate the effects of each life stage (and its associated flow components) on modelled population outcomes.

We prepared 10 scenarios. The first of these included flow-derived variation in all early life stages (the base case model). The next 4 scenarios included constant survival of a single early life stage (eggs, larvae and the 2 fingerling stages). In these scenarios, the stage with constant survival was set to the mean survival rate for that parameter in the underlying model construct. We ran each of these 5 scenarios with and without CEW in the input flow time series, giving a total of 10 scenarios (Table 2.2).

Table 2.2 List of modelled scenarios for the Murray cod model

Scenario	Model state	Environmental watering	Scenario code
1	Base case	With CEW	CEW B
2	Base case	Without CEW	wo CEW B
3	Constant egg survival	With CEW	CEW-E
4	Constant egg survival	Without CEW	wo CEW-E
5	Constant larval survival	With CEW	CEW-L
6	Constant larval survival	Without CEW	wo CEW-L
7	Constant fingerling survival (first stage)	With CEW	CEW-F1
8	Constant fingerling survival (first stage)	Without CEW	wo CEW-F1
9	Constant fingerling survival (second stage)	With CEW	CEW-F2
10	Constant fingerling survival (second stage)	Without CEW	wo CEW-F2

2.3.2 Golden perch

For the golden perch metapopulation model, life history responses to flow characteristics were modified to assess the sensitivity of model outputs to variation or uncertainty in key model processes linked to flow metrics. We focused on 4 processes: upstream:downstream movement ratios, thresholds for flow-cued spawning, larval drift responses to flow, and reduced survival under low flows. We note that the golden perch model includes a more complex set of flow associations than the Murray cod model, so that changes in these processes potentially have population- and Basin-scale impacts on modelled population outcomes. Specifically, flow characteristics directly influence several life history parameters (spawning, larval drift, juvenile and adult movement, and survival of early life stages) via a series of model rules derived from empirical data and expert opinion (Todd et al. 2022a, 2022b).

We tested model sensitivity to each process separately; and considered scenarios with and without CEW for each scenario listed in Table 2.3.

Table 2.3 List of modelled scenarios for the golden perch model

Scenario	Model state	Environmental watering	Scenario name
1	Base	With CEW	CEW B
2	Base	Without CEW	wo CEW B
3	Upstream movement increased	With CEW	CEW M+
4	Upstream movement increased	Without CEW	wo CEW M+
5	Upstream movement decreased	With CEW	CEW M-
6	Upstream movement decreased	Without CEW	wo CEW M-
7	Reduced spawning threshold	With CEW	CEW Sp+
8	Reduced spawning threshold	Without CEW	wo CEW Sp+
9	Increased spawning threshold	With CEW	CEW Sp-
10	Increased spawning threshold	Without CEW	wo CEW Sp-
11	Increased rate of larval drift	With CEW	CEW LD+
12	Increased rate of larval drift	Without CEW	wo CEW LD+
13	Reduced rate of larval drift	With CEW	CEW LD-
14	Reduced rate of larval drift	Without CEW	wo CEW LD-
15	Low flows, base case	With CEW	CEW B LF
16	Low flows, base case	Without CEW	wo CEW B LF

Scenario	Model state	Environmental watering	Scenario name
17	No low-flow conditions	With CEW	CEW LF+
18	No low-flow conditions	Without CEW	wo CEW LF+
19	Annual low flows	With CEW	CEW LF-
20	Annual low flows	Without CEW	wo CEW LF-

The existing upstream:downstream movement ratio assumes that juveniles, adults and adult spawning runs follow a 3:1 upstream to downstream ratio in the southern Basin and a 4:1 upstream to downstream ratio in the northern Basin (base case). We developed 2 scenarios based on findings of the Basin-scale Flow-MER Fish Research Theme (project F2: Fish movement): a 4.5:1 ratio in both the southern Basin and northern Basin (M+) and a 2:1 ratio in both the southern Basin and northern Basin (M-). To assess the impacts of different thresholds for flow-cued spawning, we considered 2 scenarios (as well as a base case based on the existing model construct). First, we halved the flow threshold that triggers spawning (producing an increase in spawning: Sp+), and then we doubled this threshold (producing a decrease in spawning: Sp-). To assess the influence of changes in larval drift, we increased the sensitivity of larval drift to flow (LD+: doubling the rate in most cases but capped to a maximum rate of 100%) and then decreased the sensitivity to flow (LD-: halving the rate).

Testing the sensitivity of model outputs to low flows required changes to the model construct, which did not include a specific response to low flow conditions. Specifically, we incorporated a reduction (of 20%) in survival of all life stages in any systems and years in which flows fell below a specified low-flow threshold. This updated model structure was used only for northern Basin populations because low-flow mortality is not considered a major threat for the golden perch populations modelled in the southern Basin. The specific thresholds were gathered from the literature and northern Basin watering proposals, and were used to generate flow scenarios capturing potential low-flow impacts with and without CEW (Table 2.4).

Given relatively minimal impacts of CEW on the occurrence of low flows (based on the current rules and counterfactual scenarios provided by the Flow-MER Hydrology Theme), we considered two additional scenarios of low-flow impacts (noting these were applied to northern Basin populations only): a scenario in which flows remained above the low-flow thresholds in all years (LF+) and a scenario in which flows dropped below low-flow thresholds in every year. These modified scenarios were run with and without CEW to account for potential differences in other flow-derived model parameters (Table 2.3).

Table 2.4 List of low-flow thresholds included in the revised golden perch model

Note that low-flow thresholds were included only for northern Basin populations because low-flow mortality is not considered a major threat to golden perch populations in the southern Basin.

Population number	River	Relevant gauge number	Low flow threshold	Source
8	Darling	425004	>70 ML/d for 330 days in a year	DPIE 2020a
9	Barwon	416001	>45 ML/d for 310 days in a year	DPIE 2020a
10	Gwydir	418004	>20 ML/d for 350 days in a year	DPIE 2020b
11	Warrego	432002	2 ML/d for more than 1 day in a year	CEWH 2023a
12	Culgoa	422204A	>1 ML/d for minimum of 1 day in a year	CEWH 2023b
13	Condamine-Balonne	422333A	None found in literature; adopted population 12 threshold	

2.4 Interpretation of model outputs

The population model generated 1,000 replicate trajectories for each scenario. We present mean trajectories (the average of the 1,000 replicates) for adults and 1 year old recruits, focusing primarily on a projected period of 2030–2070 for Murray cod and 2030–2075 for golden perch. We also present the expected minimum or mean population size (EMPS – the Expected Value of the distribution of minimum or mean Population Sizes) under each scenario, which is the average mean value across all 1,000 trajectories. In figures depicting EMPS values, we present percentage changes relative to the base case with an equivalent environmental water contribution (i.e. we compare scenarios containing CEW to the base case with CEW and scenarios without CEW [wo CEW] to the base case without CEW).

3 Results

3.1 Sensitivity of the Murray cod population model to changes in key processes influencing early life stage survival

Modelled population outcomes for Murray cod indicated that the flow components that influence egg survival and larval survival had a larger impact on population dynamics than the components influencing fingerling survival (Figure 3.1 to Figure 3.6). The inclusion of CEW in scenarios was associated with several minor changes, including a slightly negative response to CEW in the Lachlan and Lower Murray rivers (Figure 3.4 and Figure 3.6), no response in the Edward and Gwydir rivers (Figure 3.1 and Figure 3.3), and a slightly positive response in the Goulburn and Murrumbidgee rivers (Figure 3.2 and Figure 3.5).

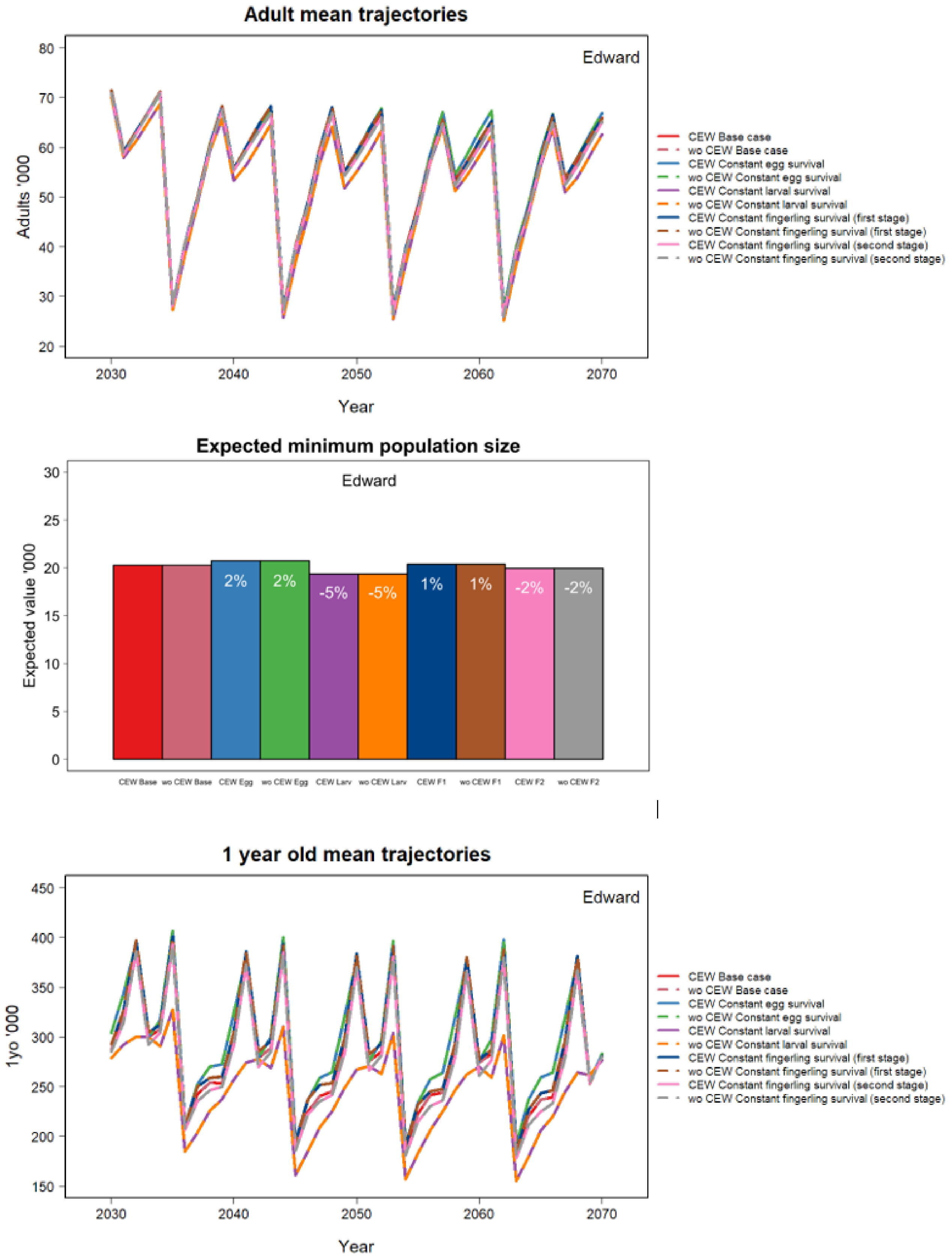
Projected population trajectories were most sensitive to variation in the flow components associated with egg survival (antecedent flow and Oct–Dec water temperature), with this pattern particularly apparent in the Gwydir River population. In the Gwydir River, setting egg survival at a constant value (i.e. disregarding variation in the flow components associated with egg survival) produced large increases in the estimated adult population size under scenarios with and without CEW (+110% expected minimum population size; Figure 3.3). This response may occur because disregarding the flow components associated with egg survival removes any negative impacts of coldwater pollution (which significantly reduced egg survival under the base case in many years in the Gwydir River).

Model outputs were slightly sensitive to variation in the flow component associated with larval survival (variability in Oct–Dec discharge). Setting larval survival at a constant value (i.e. disregarding variation in the flow component associated with larval survival) generated slight reductions in overall population outcomes in all populations except the Goulburn River. This finding may indicate that current levels of flow variability in the Selected Areas are generally beneficial for Murray cod larval survival (noting that the underlying assumption in the model construct is that larval survival is reduced by excessive flow variability; Tonkin et al. 2021).

The sensitivity of model outputs to changes in the survival of different life stages was mostly consistent in scenarios with and without CEW. Several very subtle interactions were apparent, such as minor differences in population outcomes in the Lower Murray River due to CEW except when egg survival was constant (in which case scenarios with and without CEW generated similar outcomes) (Figure 3.6).

3.1.1 Edward River

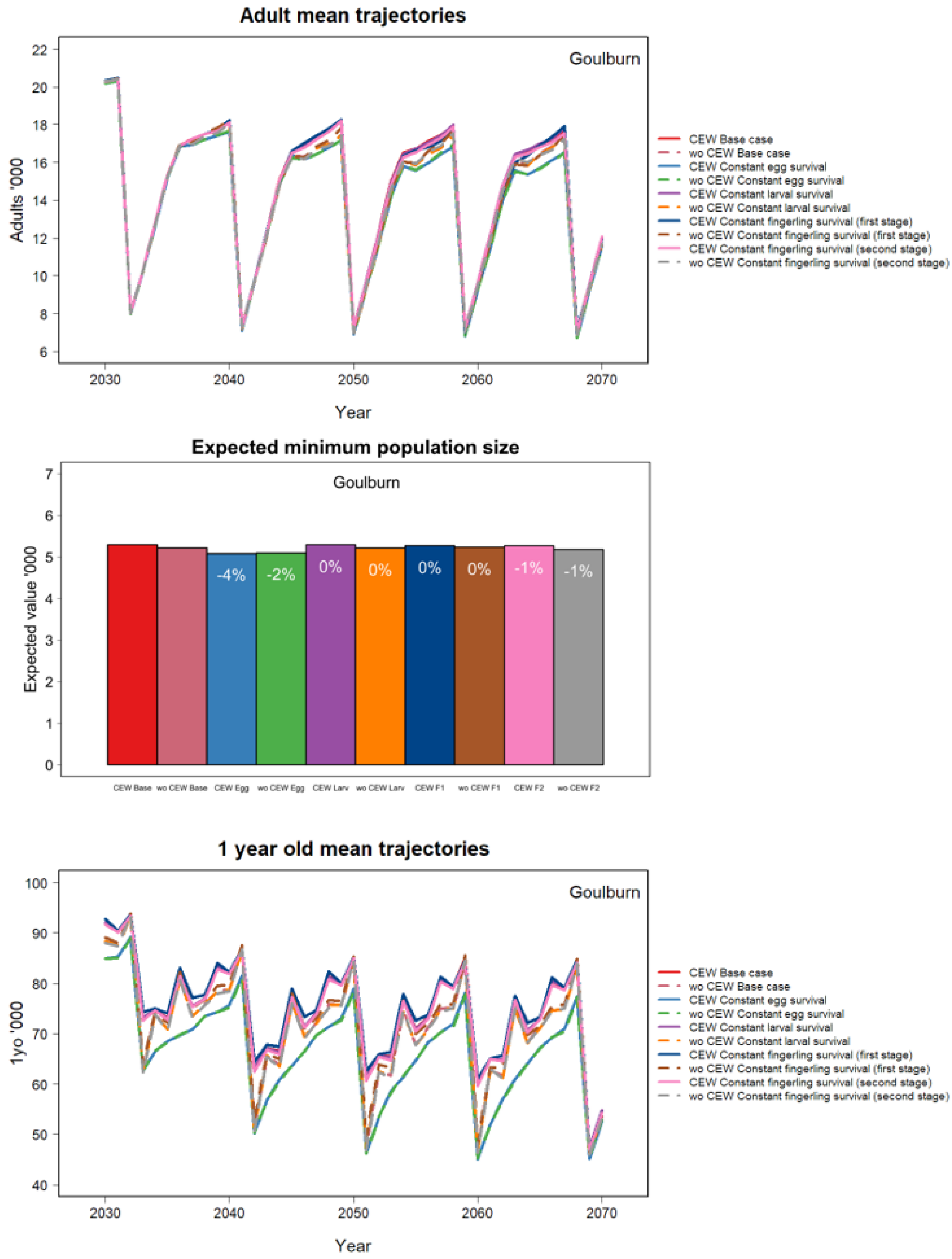
Figure 3.1 Modelled Murray cod population outcomes in the Edward River under the 10 scenarios listed in Table 2.2
The top panel shows the mean trajectory of adult fish, the middle panel shows the expected minimum adult population size under each scenario and the bottom panel shows the mean trajectory of 1-year old fish. Scenarios labelled with 'B' are base case, 'E' shows scenarios where egg survival is analysed, 'F1' is first stage of fingerling survival and 'F2' is scenarios analysing the second stage of fingerling survival. CEW and wo CEW denote scenarios with and without contributions of Commonwealth Environmental Water, respectively



3.1.2 Goulburn River

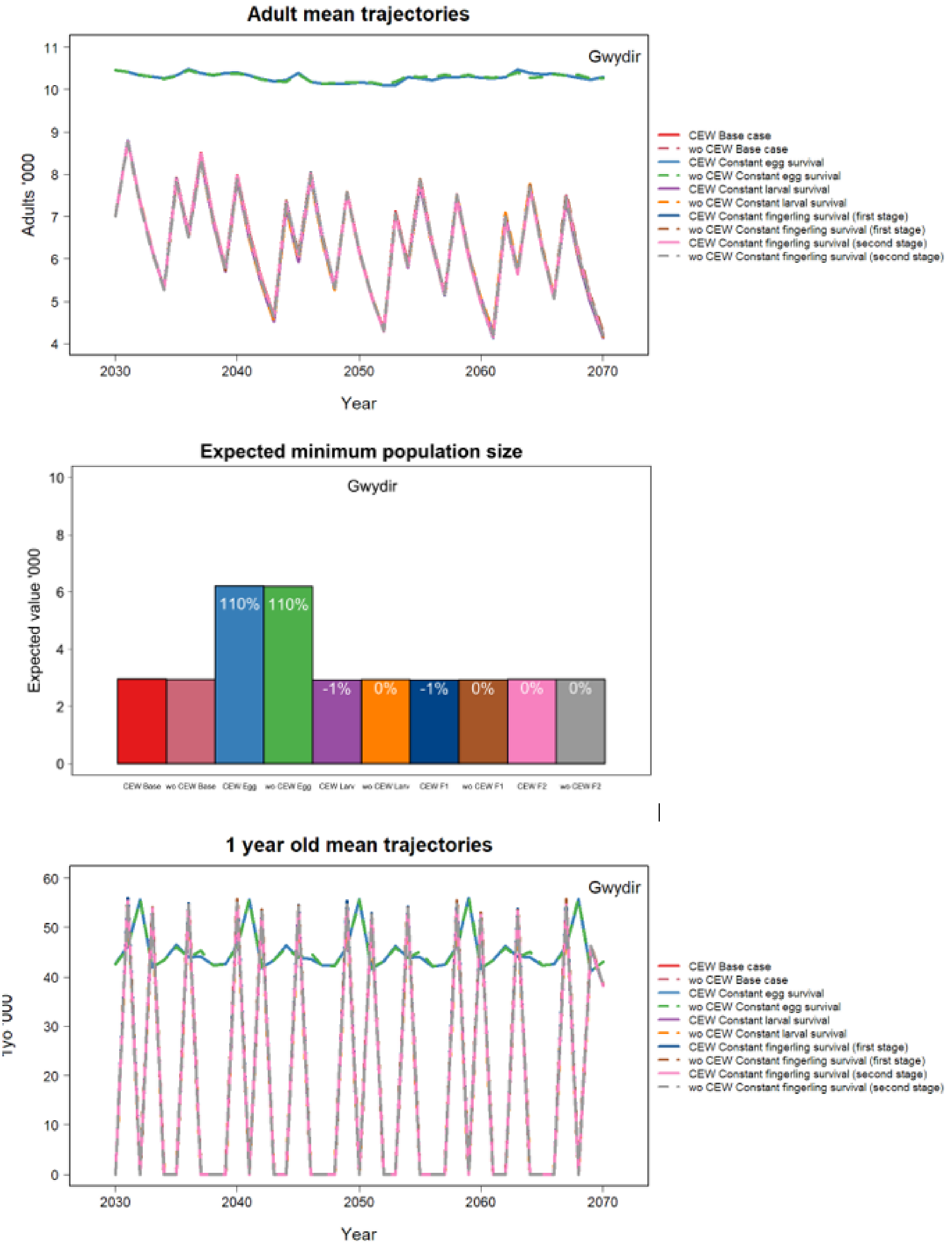
Figure 3.2 Modelled Murray cod population outcomes in the Goulburn River under the 10 scenarios listed in Table 2.2

The top panel shows the mean trajectory of adult fish, the middle panel shows the expected minimum adult population size under each scenario and the bottom panel shows the mean trajectory of 1 year old fish. Scenarios labelled with 'B' are base case, 'E' shows scenarios where egg survival is analysed, 'F1' is first stage of fingerling survival and 'F2' is scenarios analysing the second stage of fingerling survival. CEW and wo CEW denote scenarios with and without contributions of Commonwealth Environmental Water, respectively.



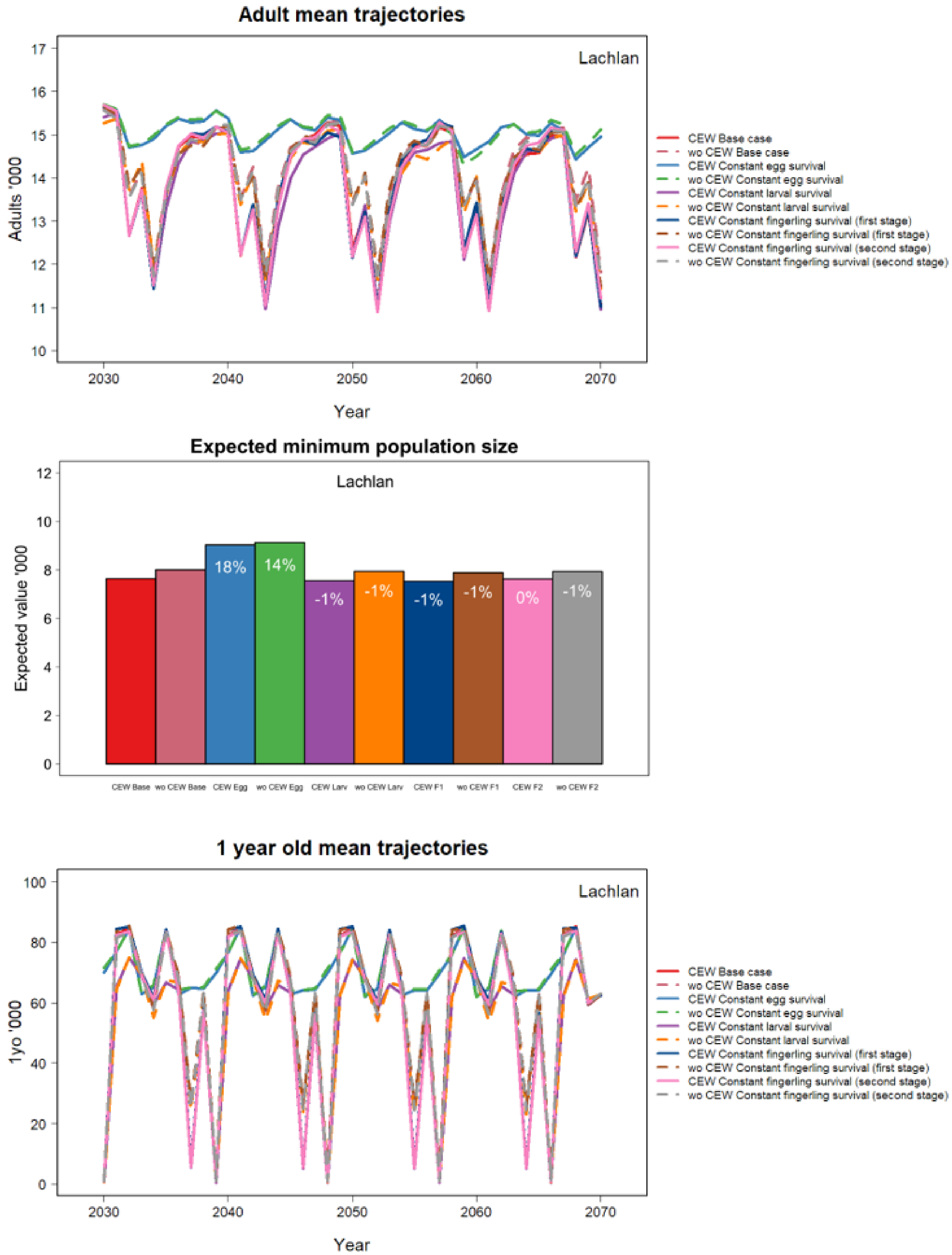
3.1.3 Gwydir River

Figure 3.3 Modelled Murray cod population outcomes in the Gwydir River under the 10 scenarios listed in Table 2.2
The top panel shows the mean trajectory of adult fish, the middle panel shows the expected minimum adult population size under each scenario and the bottom panel shows the mean trajectory of 1 year old fish. Scenarios labelled with 'B' are base case, 'E' shows scenarios where egg survival is analysed, 'F1' is first stage of fingerling survival and 'F2' is scenarios analysing the second stage of fingerling survival. CEW and wo CEW denote scenarios with and without contributions of Commonwealth Environmental Water, respectively.



3.1.4 Lachlan River

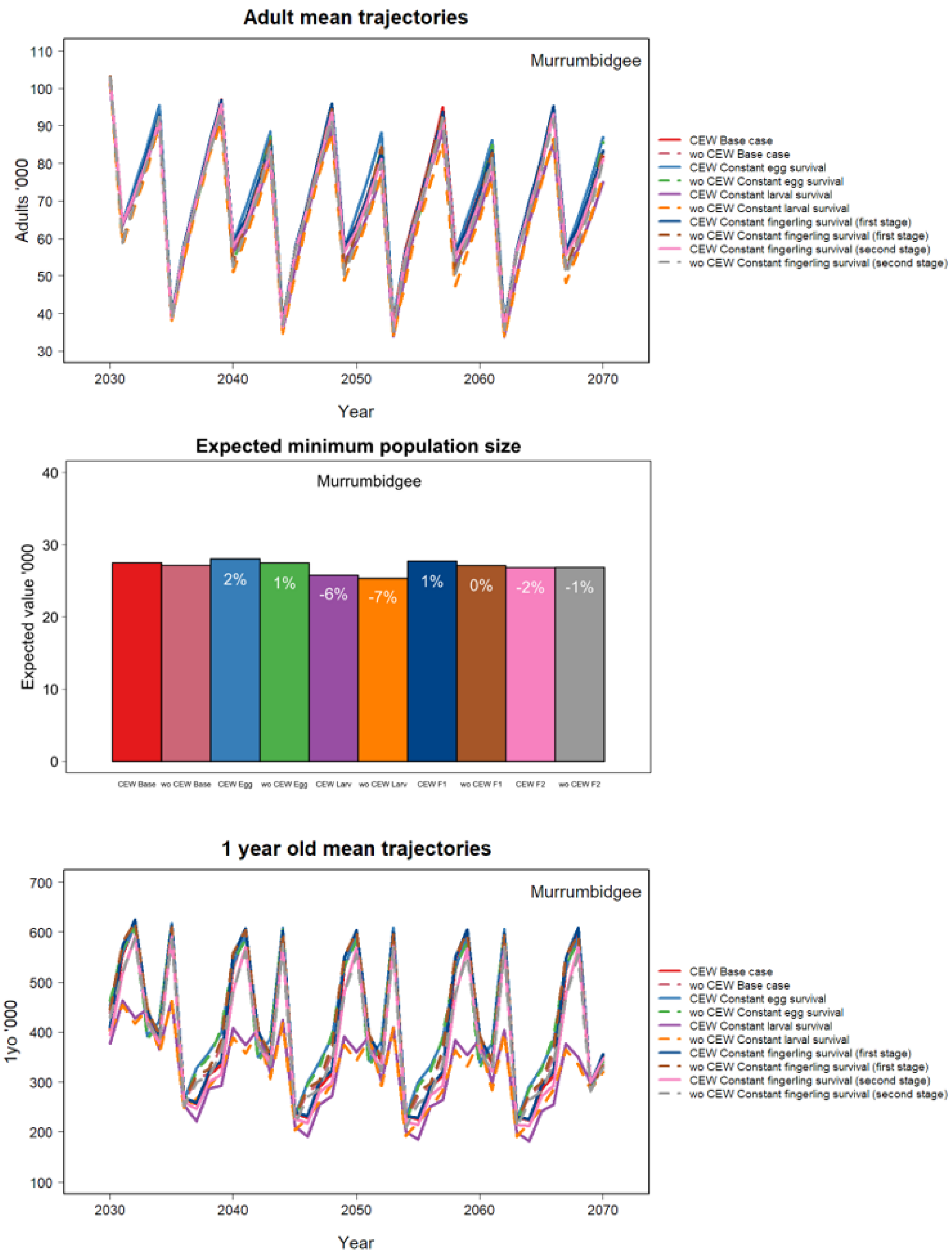
Figure 3.4 Modelled Murray cod population outcomes in the Lachlan River under the 10 scenarios listed in Table 2.2
The top panel shows the mean trajectory of adult fish, the middle panel shows the expected minimum adult population size under each scenario and the bottom panel shows the mean trajectory of 1 year old fish. Scenarios labelled with 'B' are base case, 'E' shows scenarios where egg survival is analysed, 'F1' is first stage of fingerling survival and 'F2' is scenarios analysing the second stage of fingerling survival. CEW and wo CEW denote scenarios with and without contributions of Commonwealth Environmental Water, respectively.



3.1.5 Murrumbidgee River

Figure 3.5 Modelled Murray cod population outcomes in the Murrumbidgee River under the 10 scenarios listed in Table 2.2

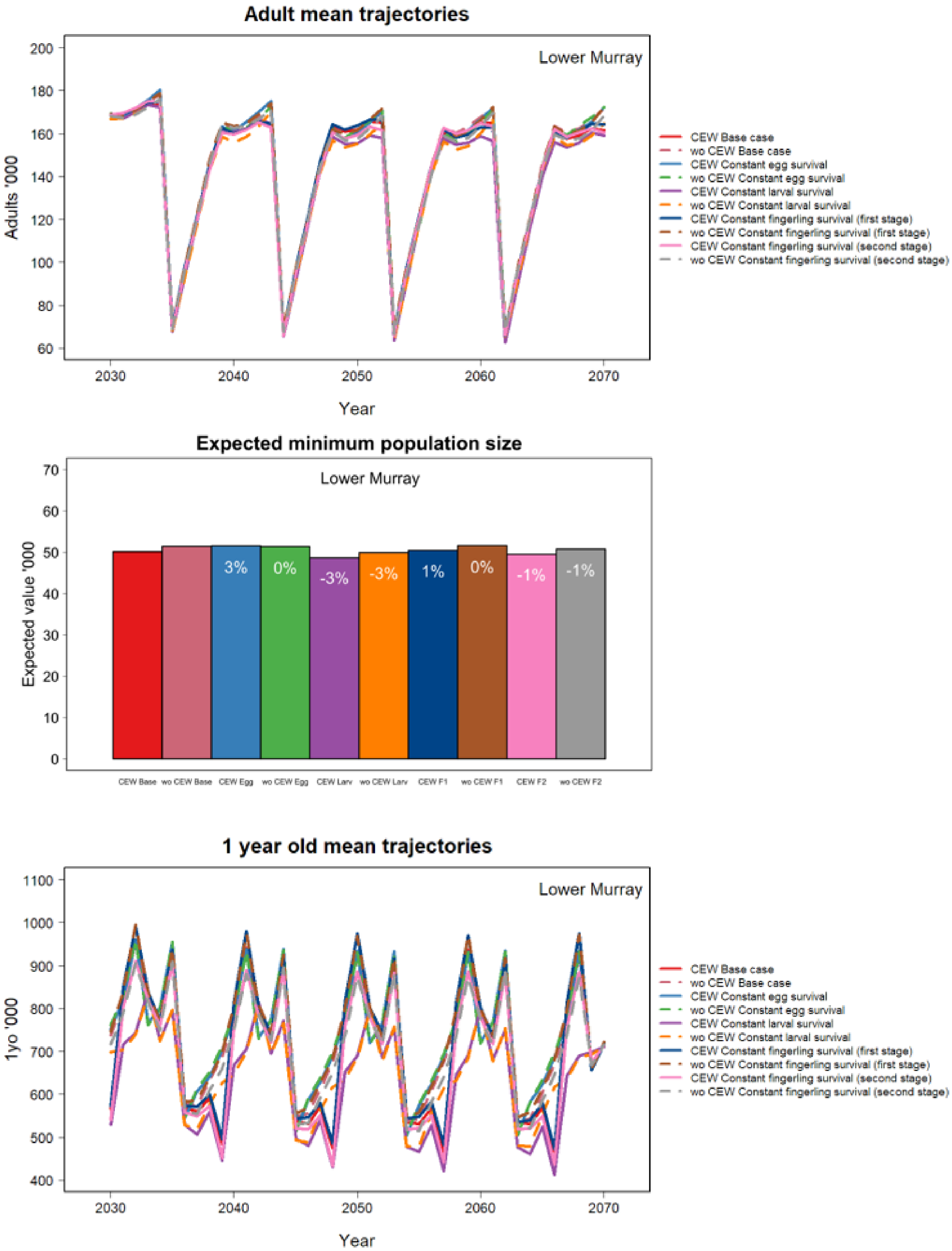
The top panel shows the mean trajectory of adult fish, the middle panel shows the expected minimum adult population size under each scenario and the bottom panel shows the mean trajectory of 1 year old fish. Scenarios labelled with 'B' are base case, 'E' shows scenarios where egg survival is analysed, 'F1' is first stage of fingerling survival and 'F2' is scenarios analysing the second stage of fingerling survival. CEW and wo CEW denote scenarios with and without contributions of Commonwealth Environmental Water, respectively.



3.1.6 Lower Murray River

Figure 3.6 Modelled Murray cod population outcomes in the Lower Murray River under the 10 scenarios listed in Table 2.2

The top panel shows the mean trajectory of adult fish, the middle panel shows the expected minimum adult population size under each scenario and the bottom panel shows the mean trajectory of 1 year old fish. Scenarios labelled with 'B' are base case, 'E' shows scenarios where egg survival is analysed, 'F1' is first stage of fingerling survival and 'F2' is scenarios analysing the second stage of fingerling survival. CEW and wo CEW denote scenarios with and without contributions of Commonwealth Environmental Water, respectively.



3.2 Sensitivity of the golden perch population model to changes in movement, spawning, larval drift, and low flow effects

The golden perch metapopulation model generated varied and complex responses under the different sensitivity scenarios, which is perhaps unsurprising given the large metapopulation construct (Figure 3.7 to Figure 3.14). Overall, the model exhibited low-to-moderate sensitivity to changes in the model rules, with a few specific exceptions. Populations in the southern Basin were generally more sensitive to changes in the rules determining spawning and larval drift, whereas populations in the northern Basin were more sensitive to changes in the rules determining movement rates and low-flow impacts (Figure 3.7 to Figure 3.14). The sensitivity of modelled population outcomes to changes in underlying processes was relatively consistent in scenarios with and without CEW (Figure 3.7 to Figure 3.14).

Increasing the ratio of upstream to downstream movement (to 4.5:1 from a base of 3:1 in the southern Basin and 4:1 in the northern Basin) increased population abundances in both the southern Basin and northern Basin (Figure 3.7, Figure 3.8), with a much greater response (9% increase) in the northern Basin (Figure 3.8). Reducing the ratio of upstream to downstream movement to 2:1 had minimal impacts on population outcomes, generating minor declines (1–2%) in EMPS in both the northern Basin and southern Basin (Figure 3.7, Figure 3.8).

Changes to the threshold for flow-cued spawning reduced golden perch population abundances in the southern Basin, regardless of whether the threshold was decreased (spawning occurs more often) or increased (spawning occurs less often) (Figure 3.9, Figure 3.10). Specifically, a reduced threshold (associated with an increase in spawning) produced small declines in estimated adult population sizes (–4% and –3%, respectively), while an increased threshold (associated with a reduction in spawning) produced larger declines (–22% and –18%, respectively). This pattern was not observed in the northern Basin, where a reduction in the threshold (increased spawning) did not affect adult population abundances, and an increase in the threshold (reduced spawning) was associated with a small increase in population abundances (+2%) (Figure 3.9, Figure 3.10).

Altering the modelled sensitivity of larval drift to flow rules generated a pattern similar to that observed when altering the spawning thresholds. Specifically, increasing the sensitivity of larval drift to flow (more larval drift) reduced population abundances in the southern Basin and northern Basin (–12% and –5%, respectively), while decreasing the sensitivity of larval drift to flow (less larval drift) generated even larger declines in abundances in the northern Basin (–8%) (Figure 3.11, Figure 3.12). By contrast, decreasing the sensitivity of larval drift to flow (less larval drift) increased modelled population abundances in the southern Basin (+9%) (Figure 3.11).

Introducing a new rule to capture potential impacts of low flows (via increased mortality of all life stages) had potentially large impacts on modelled golden perch populations (Figure 3.13, Figure 3.14). Applying the low-flow thresholds (outlined in Table 2.4) to observed flows at each location generated 1% declines in EMPS in the southern Basin and 9% declines in the northern Basin under scenarios with and without CEW (i.e. CEW does not appear to contribute to maintaining flows above the specified low-flow thresholds) (Figure 3.13, Figure 3.14). We note that low-flow rules were applied only to northern Basin populations but affect southern Basin populations via reductions in the numbers of fish moving from the northern Basin to the southern Basin. A scenario in which low flow conditions do not occur produced population outcomes equivalent to the base case (as expected) (Figure 3.13, Figure 3.14). However, a scenario in which low flows were assumed to occur in every year had relatively minor impacts on southern Basin populations (–3% EMPS) but large impacts in the northern Basin (–48% and –49% EMPS for scenarios with CEW and without CEW, respectively).

3.2.1 Golden perch model response to changes in movement

Figure 3.7 Modelled golden perch population outcomes in the southern Basin under the changes in movement scenarios listed in Table 2.3

The top panel shows the mean trajectory of adult fish, the middle panel shows the expected mean adult population size under each scenario and the bottom panel shows the mean trajectory of 1 year old fish. Scenarios labelled with 'B' are base case, 'M' shows scenarios with juvenile and adult movement sensitivity. CEW and wo CEW denote scenarios with and without contributions of Commonwealth Environmental Water, respectively.

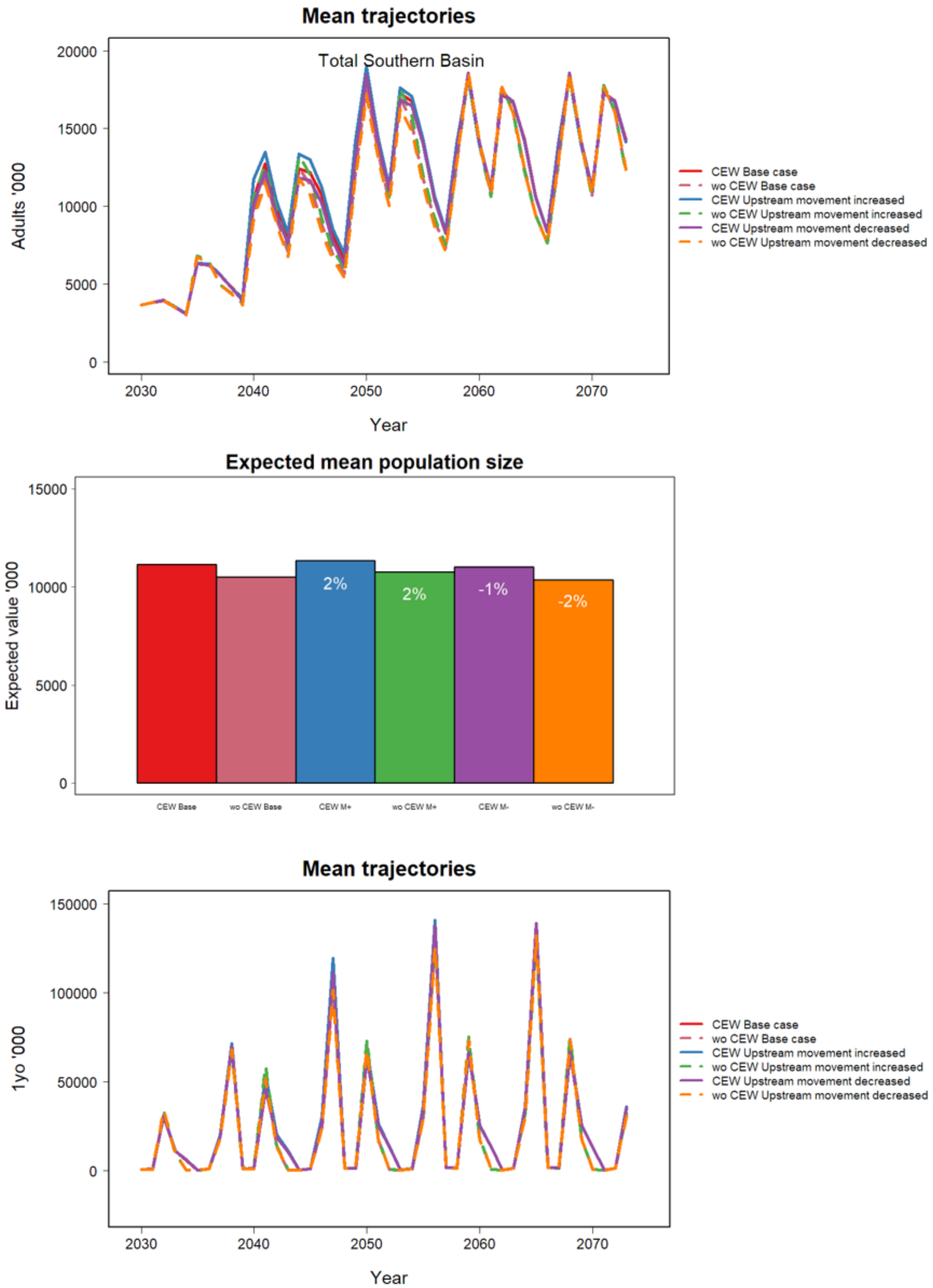
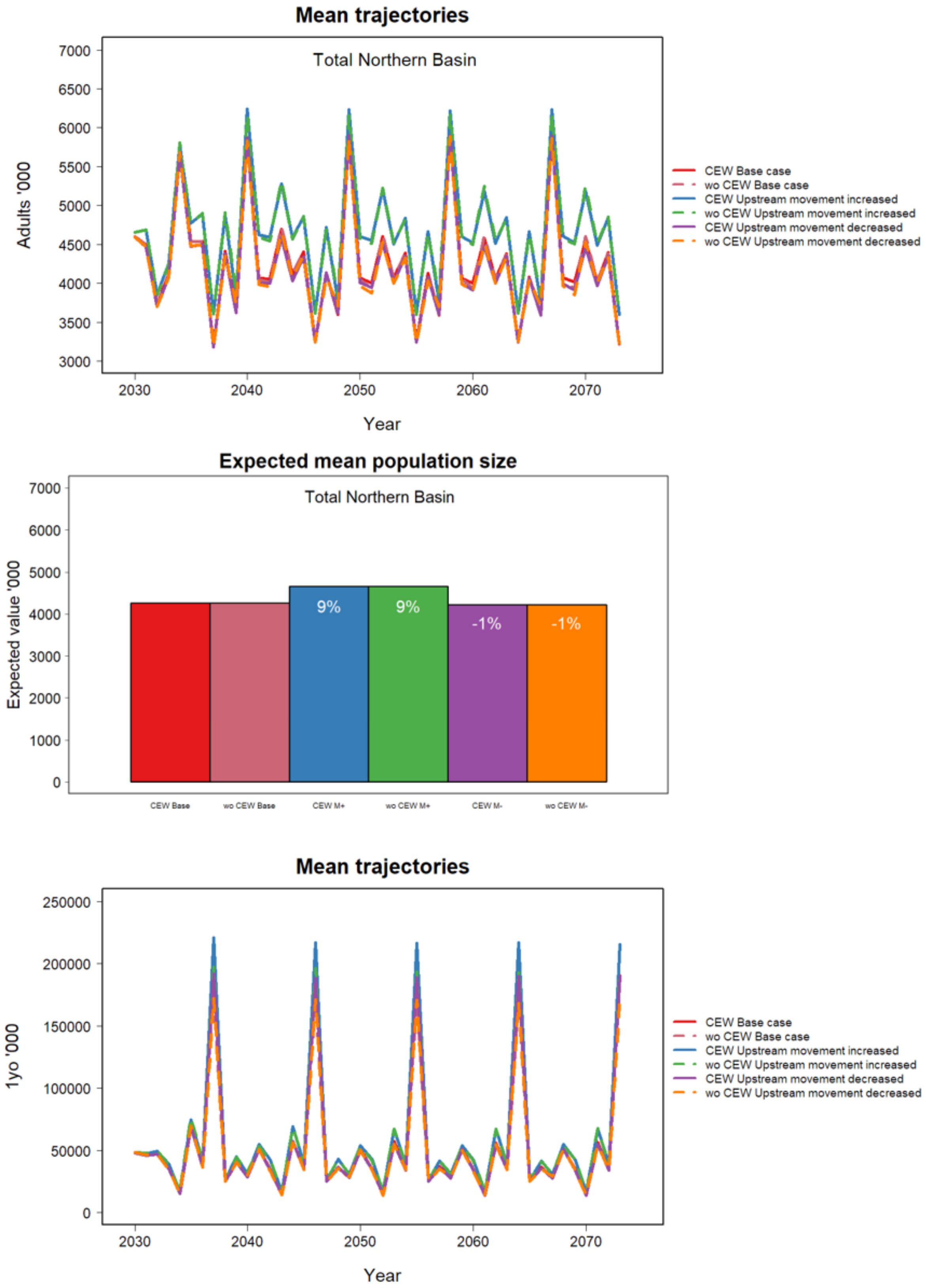


Figure 3.8 Modelled golden perch population outcomes in the northern Basin under the changes in movement scenarios listed in Table 2.3

The top panel shows the mean trajectory of adult fish, the middle panel shows the expected mean adult population size under each scenario and the bottom panel shows the mean trajectory of 1 year old fish. Scenarios labelled with 'B' are base case, 'M' shows scenarios with juvenile and adult movement sensitivity. CEW and wo CEW denote scenarios with and without contributions of Commonwealth Environmental Water, respectively.



3.2.2 Golden perch model response to changes in spawning

Figure 3.9 Modelled golden perch population outcomes in the southern Basin under the changes to spawning scenarios listed in Table 2.3

The top panel shows the mean trajectory of adult fish, the middle panel shows the expected mean adult population size under each scenario and the bottom panel shows the mean trajectory of 1 year old fish. Scenarios labelled with 'B' are base case, 'Sp' shows scenarios with spawning sensitivity. CEW and wo CEW denote scenarios with and without contributions of Commonwealth Environmental Water, respectively.

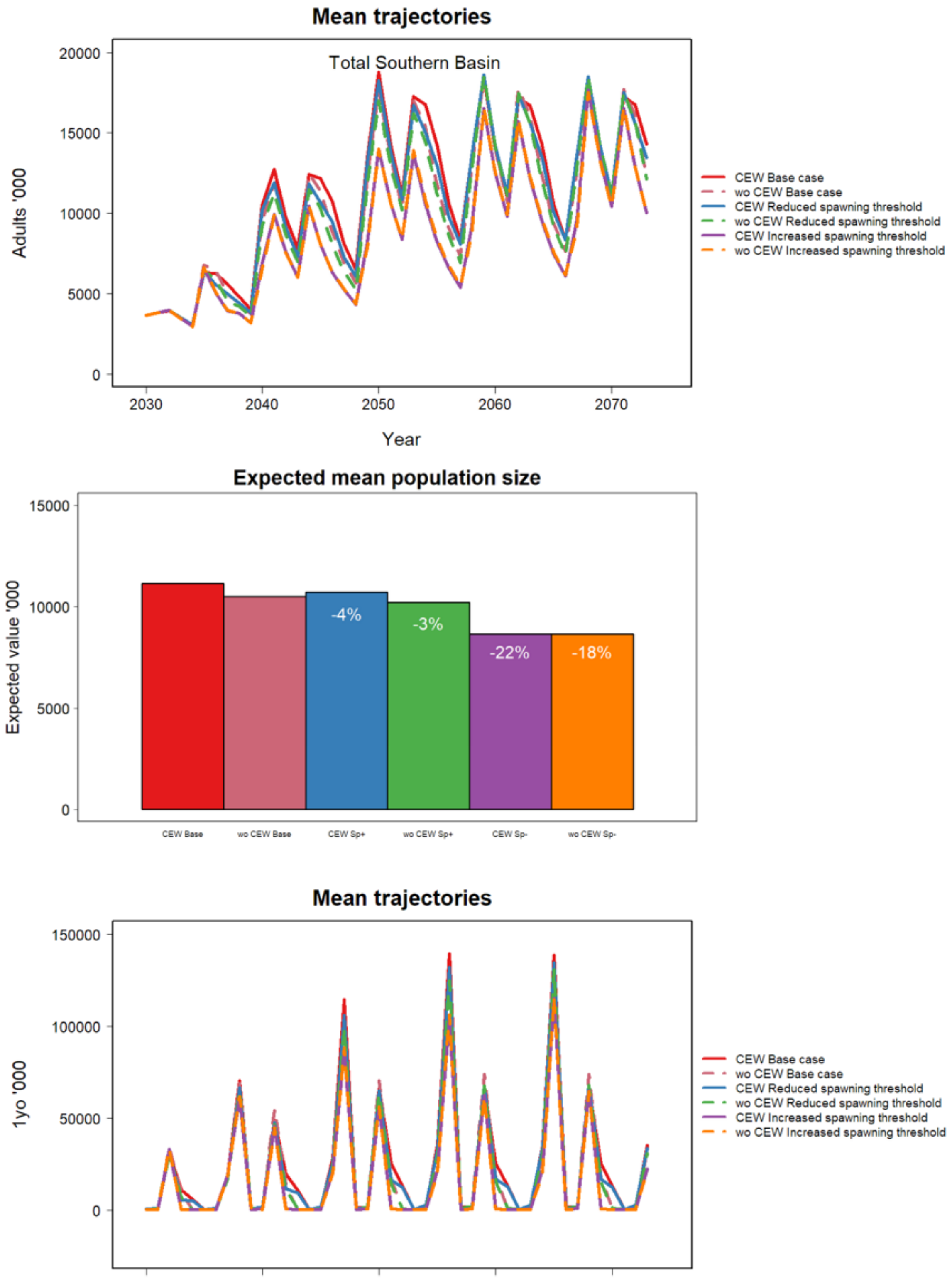
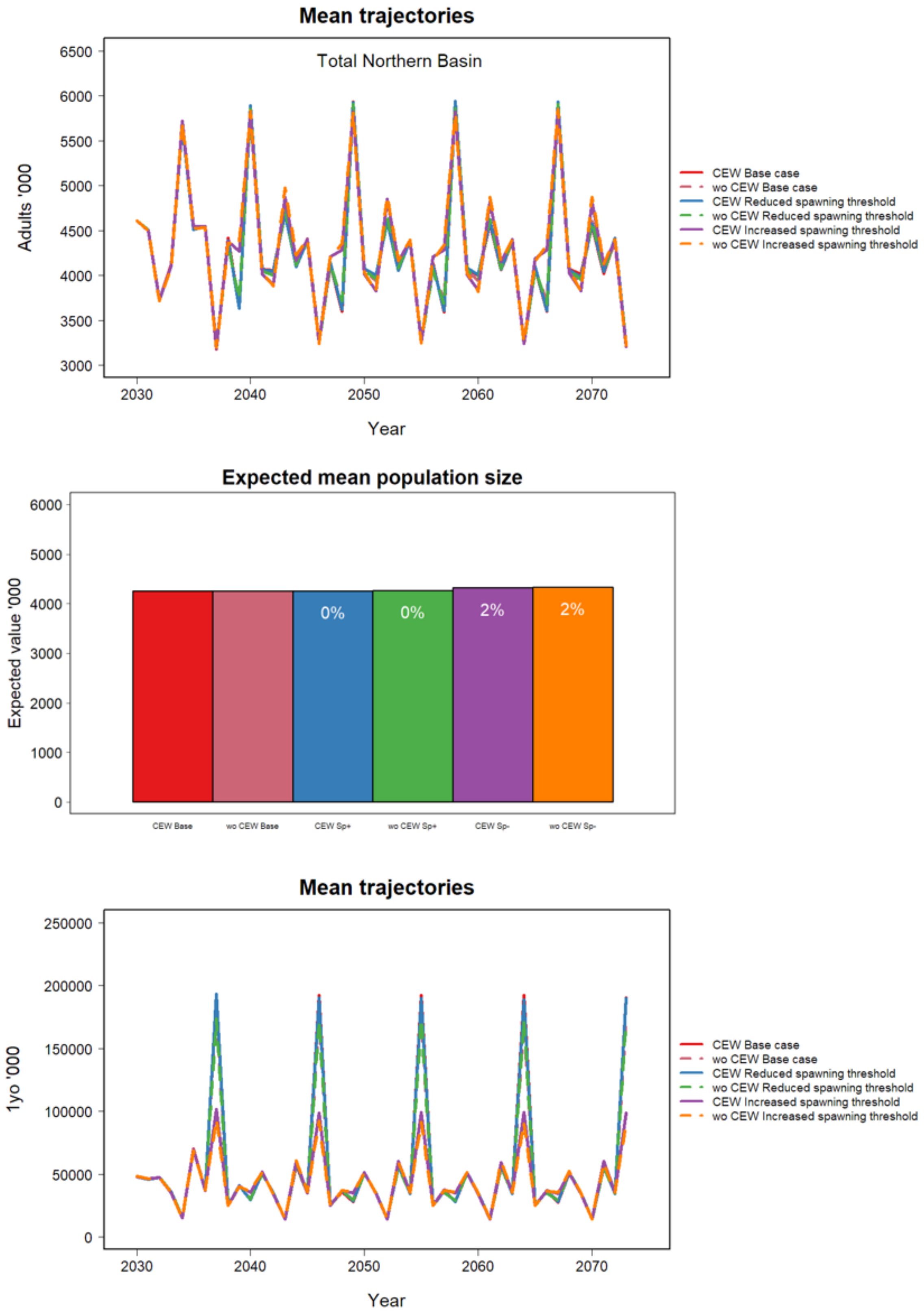


Figure 3.10 Modelled golden perch population outcomes in the northern Basin under changes in spawning scenarios listed in Table 2.3

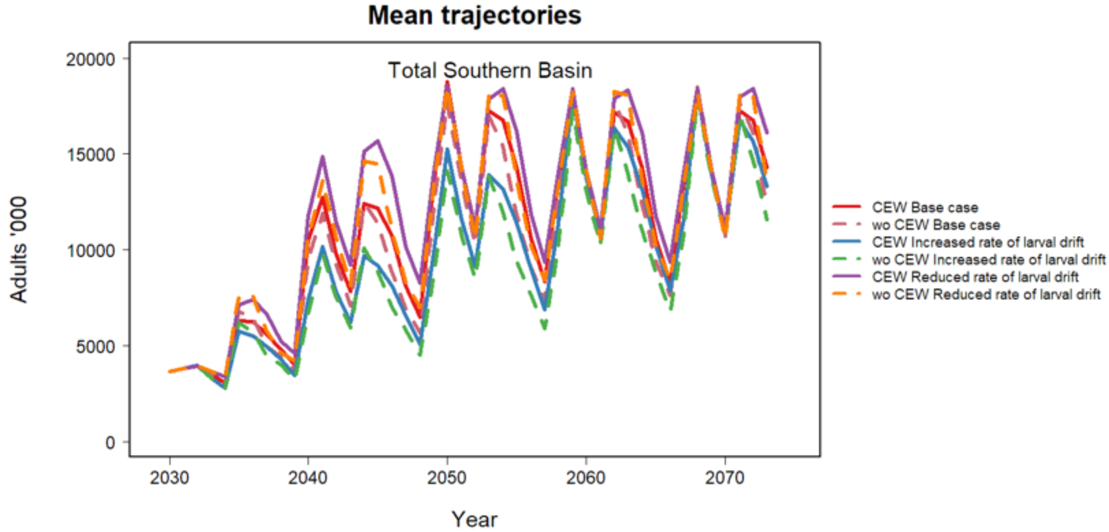
The top panel shows the mean trajectory of adult fish, the middle panel shows the expected mean adult population size under each scenario and the bottom panel shows the mean trajectory of 1 year old fish. Scenarios labelled with ‘B’ are base case, ‘Sp’ shows scenarios with spawning sensitivity. CEW and wo CEW denote scenarios with and without contributions of Commonwealth Environmental Water, respectively.

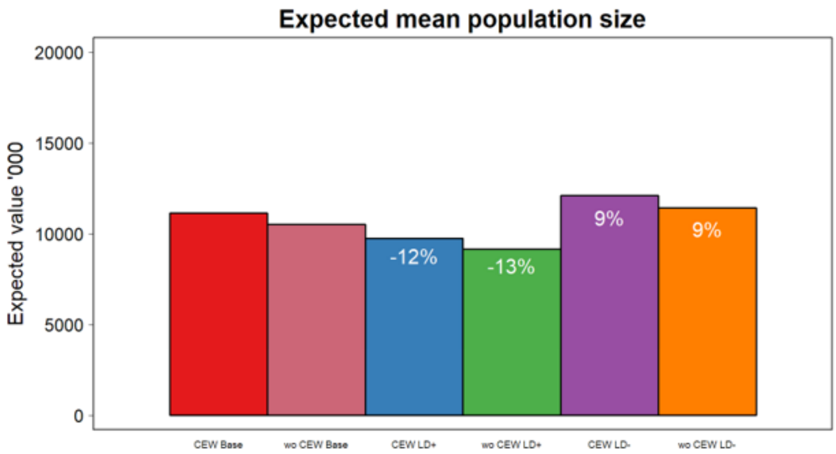


3.2.3 Golden perch model response to changes in larval drift

Figure 3.11 Modelled golden perch population outcomes in the southern Basin under the changes in larval drift scenarios listed in Table 2.3

The top panel shows the mean trajectory of adult fish, the middle panel shows the expected mean adult population size under each scenario and the bottom panel shows the mean trajectory of 1 year old fish. Scenarios labelled with 'B' are base case, 'LD' shows scenarios with larval drift sensitivity. CEW and wo CEW denote scenarios with and without contributions of Commonwealth Environmental Water, respectively.





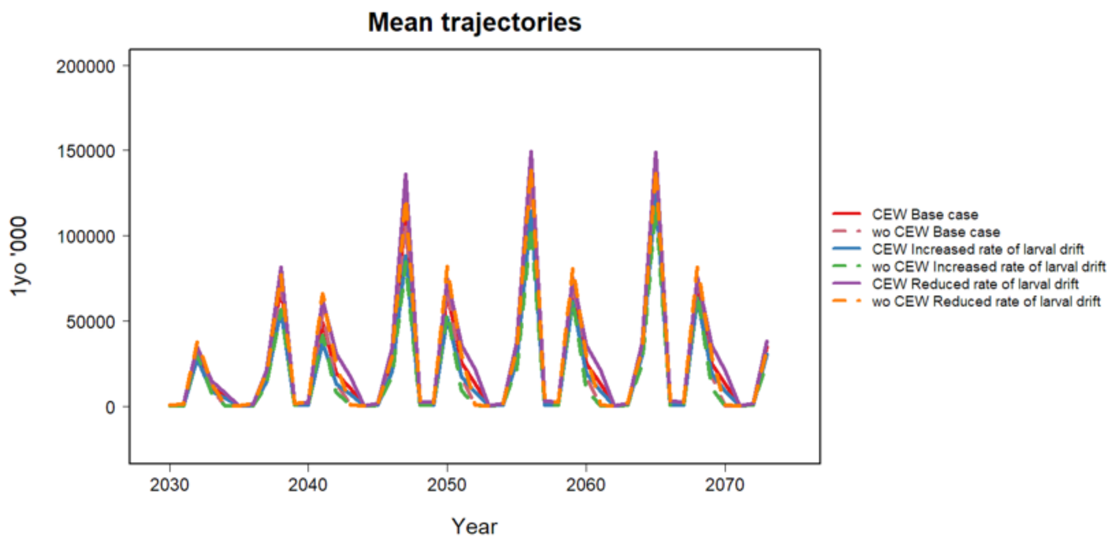
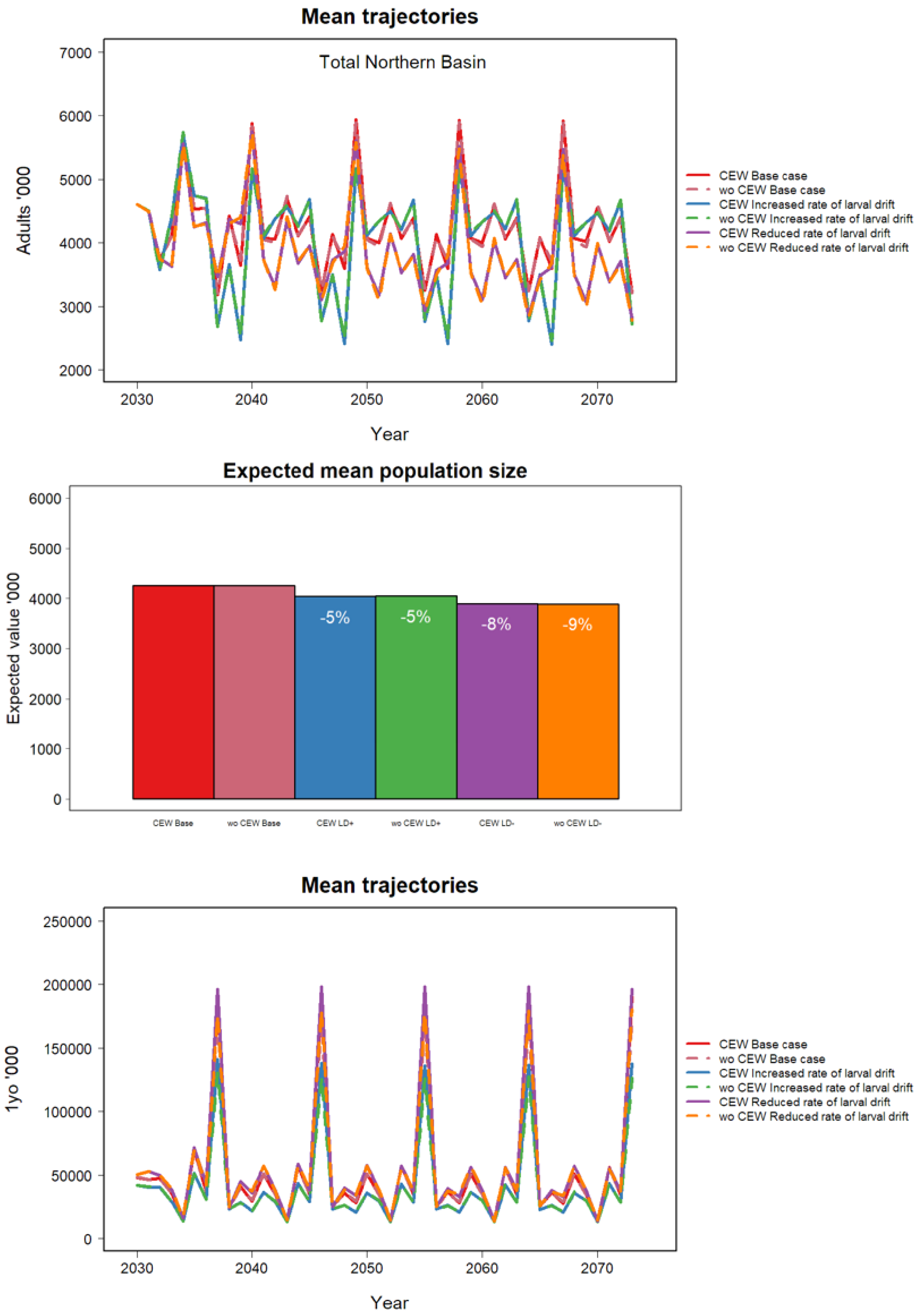


Figure 3.12 Modelled golden perch population outcomes in the northern Basin under the changes in larval drift scenarios listed in Table 2.3

The top panel shows the mean trajectory of adult fish, the middle panel shows the expected mean adult population size under each scenario and the bottom panel shows the mean trajectory of 1 year old fish. Scenarios labelled with 'B' are base case, 'LD' shows scenarios with larval drift sensitivity. CEW and wo CEW denote scenarios with and without contributions of Commonwealth Environmental Water, respectively.



3.2.4 Golden perch model response to changes in low flow threshold

Figure 3.13 Modelled golden perch population outcomes in the southern Basin under the changes in low flow threshold scenarios listed in Table 2.3

The top panel shows the mean trajectory of adult fish, the middle panel shows the expected mean adult population size under each scenario and the bottom panel shows the mean trajectory of 1 year old fish. Scenarios labelled with 'B' are base case where 'LF' shows scenarios with low flow effects and sensitivity added. CEW and wo CEW denote scenarios with and without contributions of Commonwealth Environmental Water, respectively.

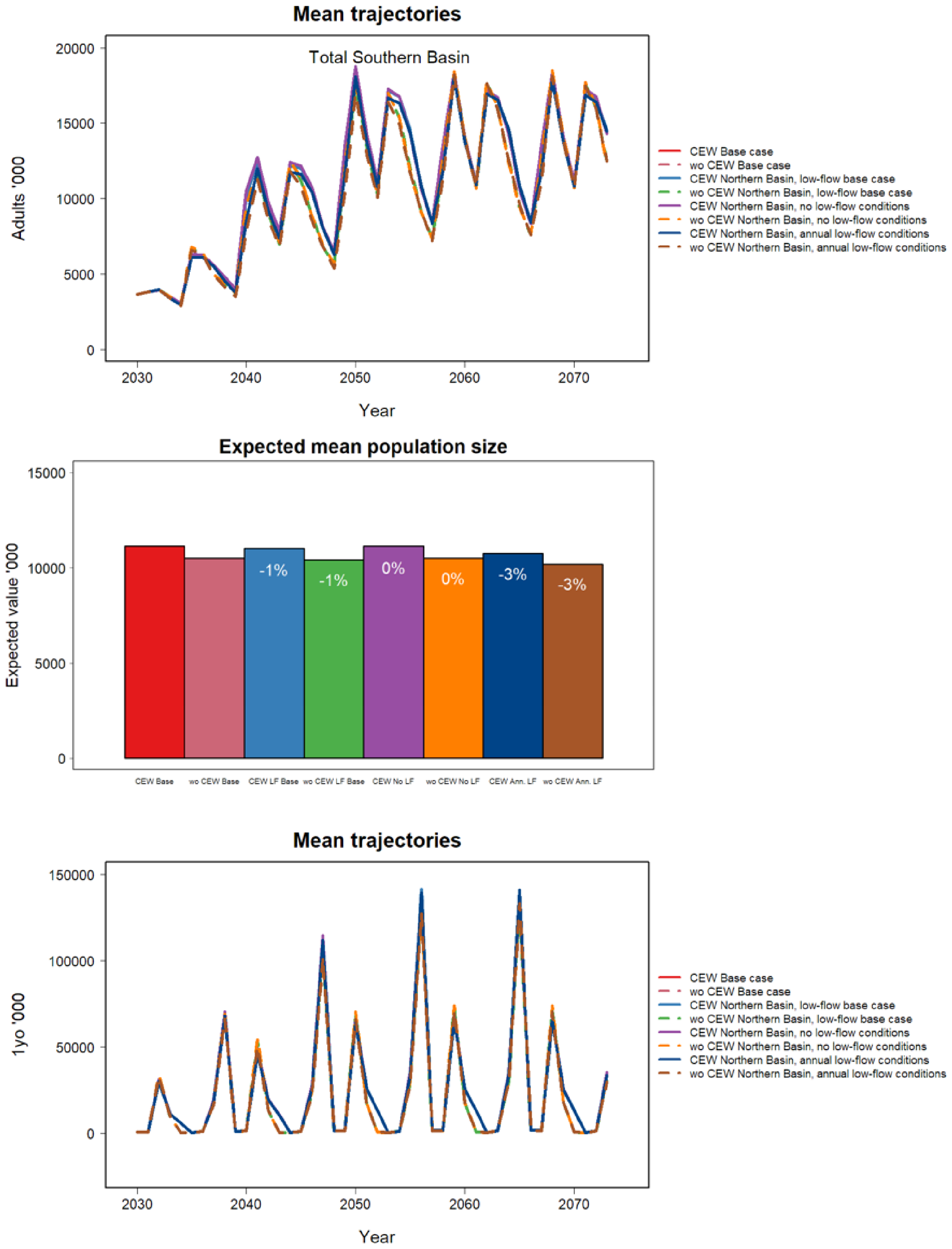
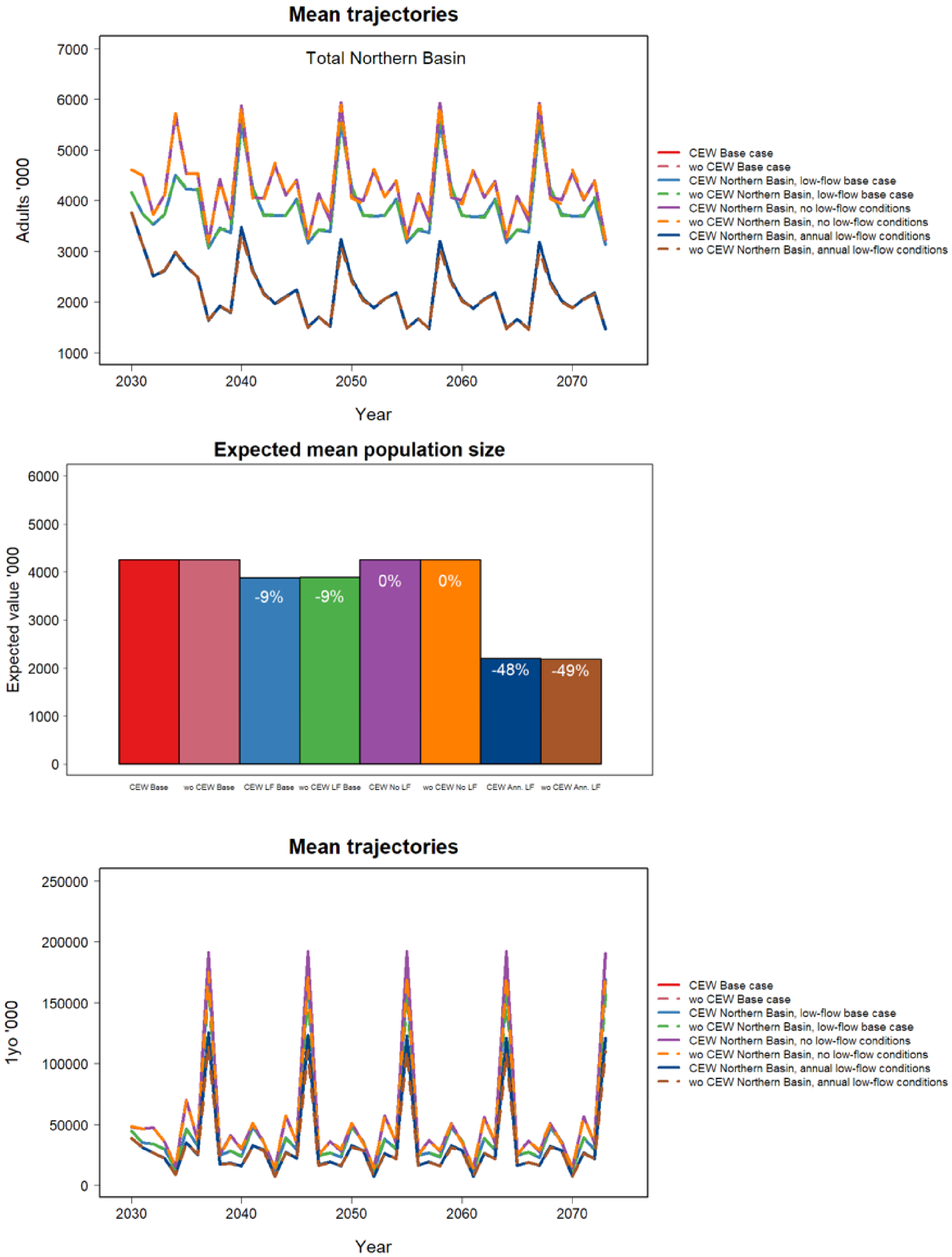


Figure 3.14 Modelled golden perch population outcomes in the northern Basin under the changes in low flow threshold scenarios listed in Table 2.3

The top panel shows the mean trajectory of adult fish, the middle panel shows the expected mean adult population size under each scenario and the bottom panel shows the mean trajectory of 1 year old fish. Scenarios labelled with ‘B’ are base case where ‘LF’ shows scenarios with low flow effects and sensitivity added. CEW and wo CEW denote scenarios with and without contributions of Commonwealth Environmental Water, respectively.



4 Discussion

The use of environmental water to support fish populations is challenging due to the broad distributions and spatial connectedness of many fish species, particularly species that occur and move across the entire Basin and are thus influenced by flow deliveries in many rivers. In earlier outputs from the Basin-scale Flow-MER Fish Research Theme, we developed a Basin-scale metapopulation model for golden perch and an Area-scale model for Murray cod (Todd et al. 2022a) and used these models to assess how fish populations respond to managed flows, including an evaluation of Basin-scale outcomes under historical scenarios with and without CEW (i.e. a counterfactual approach). Here, we used these existing models to examine the sensitivity of modelled population outcomes to variation or uncertainty in key processes, including survival of different Murray cod life stages and the rules underpinning golden perch movement, spawning, and larval drift. Alongside this sensitivity analysis, we extended the existing golden perch metapopulation model to include a low-flow threshold in the northern portion of the Basin, below which golden perch survival was reduced. We applied this threshold to the northern Basin populations only and demonstrated that model outputs were highly sensitive to the inclusion of this process and the exact specification of the low-flow thresholds.

4.1 Murray cod model response to changes in key processes influencing early life stage survival

The Murray cod model was most sensitive to variation in the flow components associated with egg and larval survival and less sensitive to variation in the flow components associated with fingerling survival.

In all Selected Areas, variation in flow had a positive influence on larval survival, which suggests that the flow conditions coinciding with the larval stage (represented by flow variability from Oct–Dec) were generally conducive to high larval survival. By contrast, variation in flow had a negative influence on egg survival, which suggests that the flow components associated with the egg stage (antecedent flows and Oct–Dec water temperatures) tended to reduce Murray cod population abundances due to a negative influence on egg survival (possibly due to the negative impacts of low water temperatures; see Section 3.1). This pattern was not observed in the Goulburn River, a system in which flows are highly controlled and stable, potentially resulting in higher Murray cod egg survival.

Sensitivity of model outputs to flow-derived egg and larval survival indicates that these stages may have a disproportionate impact on Murray cod population outcomes and, therefore, should be the focus of future model development and targeted empirical research.

Current conceptual understanding indicates that flow influences egg and larval survival primarily via its impacts on hydraulic conditions, instream productivity, and physical habitat availability during and immediately following spawning. Focusing on these conceptual pathways, key gaps in knowledge are the impacts of hydraulic conditions during and immediately following Murray cod spawning, associations between discharge (including antecedent conditions) and in-channel productivity, and the interactions of flows with physical habitat characteristics hypothesised to support Murray cod nesting and protection of early life stages (e.g. large woody habitat and instream vegetation) (Tonkin et al. 2020).

Determining the contribution of stocked fish to wild Murray cod populations would also be beneficial given these individuals do not spend their egg and larval stages in the wild and may be less susceptible to flow variation (thus following a process fundamentally different to that included in the population model).

Stocking is likely to be an important factor contributing to many of the modelled populations, and the fact that stocked individuals bypass the egg and larval survival process (i.e. all stocked individuals survive to fingerling stage) would suggest that juvenile survival may have considerable influence on the population dynamics of heavily stocked populations.

4.2 Golden perch model response to changes in key life history characteristics and low-flow thresholds

Outputs from the golden perch population model for the northern Basin were most sensitive to uncertainty in juvenile and adult upstream:downstream movement ratios and low-flow thresholds.

It is generally assumed that juvenile and adult golden perch move upstream more often than they move downstream (Thiem et al. 2022). In the initial model construct, we included ratios of upstream:downstream movement equal 3:1 in the southern Basin and 4:1 in the northern Basin. Here, we modified this rule in 2 ways, first to increase the ratio of upstream to downstream movement (4.5:1 both Basins) and second to decrease this ratio (2:1 upstream:downstream). We found that population outcomes in the northern Basin were sensitive to this movement ratio, with increases in the proportion of fish moving upstream leading to larger populations.

Combined with recent research suggesting that the proportion of golden perch moving upstream in the northern Basin increases in response to high flows or floods (J. Thiem pers. comm.), our findings suggest that flows promoting upstream movement are likely to provide metapopulation benefits for golden perch.

Low flows in the northern Basin are expected to have a strong negative influence on the survival of golden perch (Koehn et al. 2020, Mallen-Cooper and Zampatti 2020). However, the initial development of the Basin-scale metapopulation model for golden perch was focused primarily on southern Basin rivers and did not resolve the potential impacts of low flows on golden perch in the northern Basin. Here, we developed a low-flow component for the northern Basin golden perch model and parameterised this using existing flow targets as presented in water management plans for the northern Basin (cited in Table 2.4). These low-flow targets were developed by local waterway managers and are not specific to golden perch, which introduces uncertainty in the processes underpinning the targets and their relevance to golden perch population dynamics.

Golden perch populations were predicted to respond negatively to an increase in low flows, particularly in the northern Basin (as expected) but also in the southern Basin due to reductions in individuals moving from the northern to southern Basin. This finding reinforces the Basin-scale nature of golden perch population dynamics, highlighting that population outcomes in the northern Basin influence southern Basin populations via downstream connection at Menindee. Although the specification of this low-flow component of the model is preliminary, our findings suggest that low flows may have significant impacts on golden perch populations in the northern Basin, with CEW potentially playing an important role in ameliorating these impacts. The development of the low-flow component revealed several gaps in our knowledge of low flows, including the thresholds that constitute low flows in each system, the contribution of delivered water (including CEW) to maintaining flows above these thresholds, and the importance of the timing and duration of any low flow events for fish populations, including golden perch.

Modelled golden perch population dynamics in the southern Basin were most sensitive to uncertainty in spawning and larval drift. The rules underpinning spawning and larval drift in the golden perch model were derived from expert knowledge and are subject to moderate levels of uncertainty (see Todd et al. 2022a, 2023). Modifying the thresholds for flow-cued spawning generated unexpected results, with both increases or decreases to these thresholds leading to reductions in golden perch populations. The exact cause of this pattern is unclear, and highlights a challenge of working with highly complex, process-explicit models. Further interrogation of the model would be required to determine the impacts of altered spawning thresholds on metapopulation outcomes, with these impacts likely mediated by interactions between spawning, larval drift, movement, and density dependence across multiple connected populations.

Similarly, altering the flow threshold for larval drift generated a mix of expected and unexpected outcomes. In the southern Basin (and as expected), increasing this threshold (expected to reduce the rate of larval drift) reduced total population abundances and decreasing this threshold (expected to increase the rate of larval drift) increased population abundances. By contrast, changes in the flow threshold for larval drift reduced population abundances in the northern Basin irrespective of whether the threshold was increased or decreased (albeit with a larger effect when decreasing the threshold). Examining individual population trajectories in the northern Basin suggests that this negative response may be driven by the Culgoa and Condamine-Balonne populations, where increases in retained larvae can combine with poor recruitment to generate a negative outcome in those populations under a range of scenarios. However, as outlined above in relation to spawning thresholds, a nuanced interrogation of the model would be required to fully resolve the underlying mechanisms.

4.3 Recommendations and key findings

It is perhaps unsurprising that population model outcomes were sensitive to the assumptions underpinning the models. More important is the identification of specific processes or life stages for which variation or uncertainty in parameters has a disproportionate impact on modelled outcomes. Here, we identified egg and larval survival (and associated flow components) as key determinants of Murray cod population outcomes, with uncertainty in these parameters likely to have large impacts on modelled population dynamics. Similarly, the golden perch metapopulation model was sensitive to all tested processes, but the relative influence of these processes differed between the northern and southern Basin. This finding suggests that the existing golden perch model, derived from expert knowledge from across the Basin, requires nuanced revisions specific to each region. Importantly, our study revealed that uncertainty in processes occurring in one region (e.g., in the northern Basin) has the potential to affect population outcomes elsewhere in the Basin, which highlights the Basin-scale nature of golden perch populations (and our metapopulation model).

Although our analysis identified some differences in population outcomes in scenarios with and without CEW, the sensitivity of model outcomes to key parameters did not markedly affect the predicted outcomes of CEW. This finding was consistent for both Murray cod and golden perch models, and suggests that the current counterfactual approach (i.e. estimating population outcomes under scenarios with and without CEW) is robust to uncertainty in model assumptions.

This finding provides confidence that population models, including the Basin-scale golden perch model, are appropriate tools to assess the contributions of CEW to improving native fish populations in the Basin.

Based on our findings, we provide the following recommendations:

1. Incorporate population models in the Flow-MER fish evaluation. Embedding population models in evaluations would support a quantitative assessment of population outcomes with and without CEW and would provide greater opportunities to implement and validate the population models. In particular, and as demonstrated in earlier outputs of the Flow-MER Fish Research Theme (project F1: Fish population models), the Basin-scale golden perch model provides a unique opportunity to assess Basin-scale outcomes of CEW (including outside of Selected Areas).
2. High sensitivity of modelled Murray cod population outcomes to variation in the flow components associated with egg and larval survival indicates a need to develop targeted research projects to strengthen understanding of the early life history of Murray cod. Key flow components identified in the sensitivity analysis include flow variability and water temperatures from Oct–Dec and antecedent flow conditions. Current conceptual understanding of these flow components indicates that they influence Murray cod via their impacts on hydraulic conditions, instream productivity, and physical habitat availability during and immediately following spawning. Improving the availability of data on these factors and knowledge of their links to Murray cod population dynamics will require greater collaboration among Flow-MER Themes.
3. High sensitivity of modelled golden perch population outcomes to early life stages (eggs and larvae) in the southern Basin and juvenile and adult stages in the northern Basin suggests a need to complement the Basin-scale golden perch model with empirical research examining differences in golden perch population dynamics across the Basin. Empirical research has previously been used to refine and validate the golden perch model in the southern Basin (with a particular focus on movement rules among populations). Further empirical work could address remaining uncertainties around egg and larval drift, as well as movement rules and low-flow impacts in the northern Basin (see Recommendation 4, below). Empirical data would additionally support efforts to evaluate Basin-scale outcomes of CEW independently of the population model.
4. Quantify low-flow impacts on golden perch survival to refine low-flow thresholds for golden perch. The model currently incorporates flow recommendations for the northern Basin and reduces survival of all age classes when the low-flow threshold is not met (i.e., when flows are too low). However, it is likely that flows affect golden perch populations at levels above this threshold. In addition, the duration of low flows is likely to interact with the magnitude of these flows, and the impacts of different magnitude-duration combinations on golden perch populations is not currently well understood. Clarification of the processes underpinning low-flow thresholds in the northern Basin is also required. This includes determining fundamental thresholds below which fish survival is reduced, as well as determining the contributions of different water deliveries (including but not limited to environmental water) to exceeding the low-flow thresholds in the northern Basin.

Appendix A Population model descriptions

The following text is summarised from Todd et al. (2022a, 2022b) and is provided here for completeness. We refer readers to Todd et al. (2022a, 2022b) for further details of model development.

A.1 ESSENTIAL population modelling software

All models were developed and implemented in the software package ESSENTIAL (Todd and Lovelace 2019). ESSENTIAL enables both experts and non-experts to generate population model outputs and to assess outcomes.

A.2 Murray cod

A.2.1 Murray cod single population construct

The model summarises the life history of Murray cod by explicitly representing 50 age classes (Koehn and Todd 2012). A pre-breeding census construction is implemented (Burgman et al. 1993), with entry into the first age class (1-year age step) combining spawning, egg, larval and early juvenile survival, where early juvenile fish are defined as those less than 1 year old. Beyond 1 year of age, the survival rates define the transitions to each subsequent age class (up to 50 years). Murray cod are assumed to become sexually mature at 5 years of age, with fecundity increasing depending on the maximum size of fish in the population (see the Murray cod fecundity relationships derived for this study; Rowland 1998a, 1998b). The model only accounts for females, as males are not considered to limit the population in any way (Todd et al. 2005; Koehn and Todd 2012), although it is recognised that males are likely to play an integral role in the successful development of eggs hatching into larvae (Rowland 1998a, 1998b). A 1:1 sex ratio is assumed. While the model only accounts for females, the output is presented as total adults (male and female) by simply increasing the results by a factor of 2.

Both demographic and environmental stochasticity are included in the model (Akçakaya 1991; Todd and Ng 2001). Demographic stochasticity is incorporated using a binomial distribution to model the number of individuals surviving between consecutive time steps, and a Poisson distribution to model recruitment to the 1-year-old age class. Environmental stochasticity is incorporated by randomly varying the survival and fecundity rates each year. Survival rates were drawn from normal distributions transformed to the unit interval (Todd and Ng 2001), with specified means and standard deviations. Age-specific fecundities were drawn from a relationship estimated from hatchery data (Rowland 2005) and age–length data, with specified means and standard deviations. Todd and Ng (2001) provide a methodology for specifying correlations among survival rates; however, no information exists to quantify these correlations. Given the aquatic habitat in which fish live, it is reasonable to assume that the correlations are likely to be positive and close to unity. We assume that survival rates perfectly correlate with each other and independent of fecundity rates, where fecundity rates are perfectly correlated with each other (Todd et al. 2004).

The model includes processes for modelling the effects of density dependence, with the long-term average abundance set by the user at specific levels in each reach area. The form of density dependence used in the population model is based on the average population size that the system of interest can support over the long term. This is not a carrying capacity as such, as the density-dependence mechanism is designed to allow the population to exceed the threshold, with increasingly strong negative density dependence as the population size exceeds this threshold. The density dependence mechanisms mostly apply to 1-, 2-, and 3-year-old fish, which may reflect competition for food and habitat (see e.g. Todd and Koehn 2009; Koehn and Todd 2012).

The following equations define a Murray cod population as specified by the population model:

$$FN_{i+1,t+1} = Bin\left(FN_{i,t}, dens_{i,t} \times BW_{j,t} \times S_{i,t}\right), \qquad i = 1 \ldots 49$$

$$FN_{1,t+1} = Poisson\left(S_{0,t} \times TE_{l,t} \times S_{l,t} \times TE_{e,t} \times S_{e,t} \times 0.5 \times EggNum_t\right)$$

$$EggNum_t = \sum_{i=5}^{i=50} Fec_{i,t} \times FN_{i,t}$$

$$N_{i,t} = 2 \times FN_{i,t}$$

$$dens_{i,t} = \begin{cases} AFPS \Big/ \sum_{k=25}^{k=50} FN_{k,t}, \text{ for } i = 25 \ldots 50 \text{ and } \sum_{k=25}^{k=50} FN_{k,t} > AFPS \\ AFPS \Big/ \sum_{k=15}^{k=50} FN_{k,t}, \text{ for } i = 15 \ldots 24 \text{ and } \sum_{k=15}^{k=50} FN_{k,t} > AFPS \\ AFPS \Big/ \sum_{k=10}^{k=50} FN_{k,t}, \text{ for } i = 10 \ldots 14 \text{ and } \sum_{k=10}^{k=50} FN_{k,t} > AFPS \\ AFPS \Big/ \sum_{k=i}^{k=50} FN_{k,t}, \text{ for } i = 2 \ldots 9 \text{ and } \sum_{k=i}^{k=50} FN_{k,t} > AFPS \\ 4 \times AFPS \Big/ \sum_{k=1}^{k=50} FN_{k,t}, \text{ for } i = 1 \text{ and } \sum_{k=1}^{k=50} FN_{k,t} > 4 \times AFPS \\ 1, \end{cases}$$

$$BW_{j,t} = BW_t \qquad j = i > 3$$

$$Length_{i,t} = MaxL_t \times \left(1 - \exp(-k_t \times \left(i + 1.535\right)\right) \qquad i = 5, \ldots, 50$$

$$MaxL_t \sim N\left(ML, 40 \times ML / L_\infty\right)$$

$$L_\infty = 1360.465$$

$$k_t \sim 0.0674 + \beta\left(849.86, 884.55\right) - 0.49$$

$$Weight_{i,t} = \exp\left(a_t\right) / 1000 \times Length_{i,t}^{3.36} \qquad i = 5, \ldots, 50$$

$$a_t \sim N\left(-13.52, 0.1352\right)$$

$$Fec_{i,t} = -x_t + y_t \times Weight_{i,t} - 69.5 \times Weight_{i,t}^2 \qquad i = 5, \ldots, 50$$

$$x_t \sim N\left(389, 2723\right)$$

$$y_t \sim N\left(5344, 53.44\right)$$

where *t* is an annual time interval, $FN_{i,t}$ and $N_{i,t}$ are the numbers of female adults and total adults, assuming an even sex ratio, in the i_{th} age class at time *t*; $S_{i,t}$ is a random variate describing environmental variation in the survival rates of Murray cod in the i_{th} age class drawn from normal distributions transformed to the unit interval (Todd and Ng 2001), with no loss of information from the specified means and standard deviations; $S_{0,t}$, $S_{l,t}$, and $S_{e,t}$ are random variates describing environmental variation in survival rates of Murray cod less than 1 year old, larvae, and eggs, respectively, similar to age-specific survival, where survival rates across all ages and stages are perfectly correlated; $TE_{l,t}$ is the proportional effect of temperature on survival of larvae, and $TE_{e,t}$ is the proportional effect of temperature (see Todd et al. 2005); $dens_{i,t}$ is the density-dependence factor for adults based on the total number of adults; $BW_{j,t}$ is the blackwater effect at time *t*, where *j* are fish greater than 3 years old; $EggNum_t$ is the total number of eggs produced at time t; AFPS is the average fish population size; $Fec_{i,t}$ is the fecundity for Murray cod in the i_{th} age class, based on the age–length and length–fecundity relationships in Rowland (1998a, 1998b), where age–fecundity is perfectly correlated but not with survival (see Figure A.1 and Figure A.2); $Bin(n,s)$ is a random variate representing demographic variation in transition from one age class to the next, and it has a binomial distribution $Bin(n,s) = X\sim\text{Binom}(n,s)$, and $Poisson(m)$ is a random variate representing demographic variation in recruitment, and it has a Poisson distribution $Poisson(m) = X\sim\text{Poi}(m)$.

Figure A.1 Age–fecundity used in the population model when the average maximum size of Murray cod is 900 mm; this relationship is for smaller systems such as the Severn River

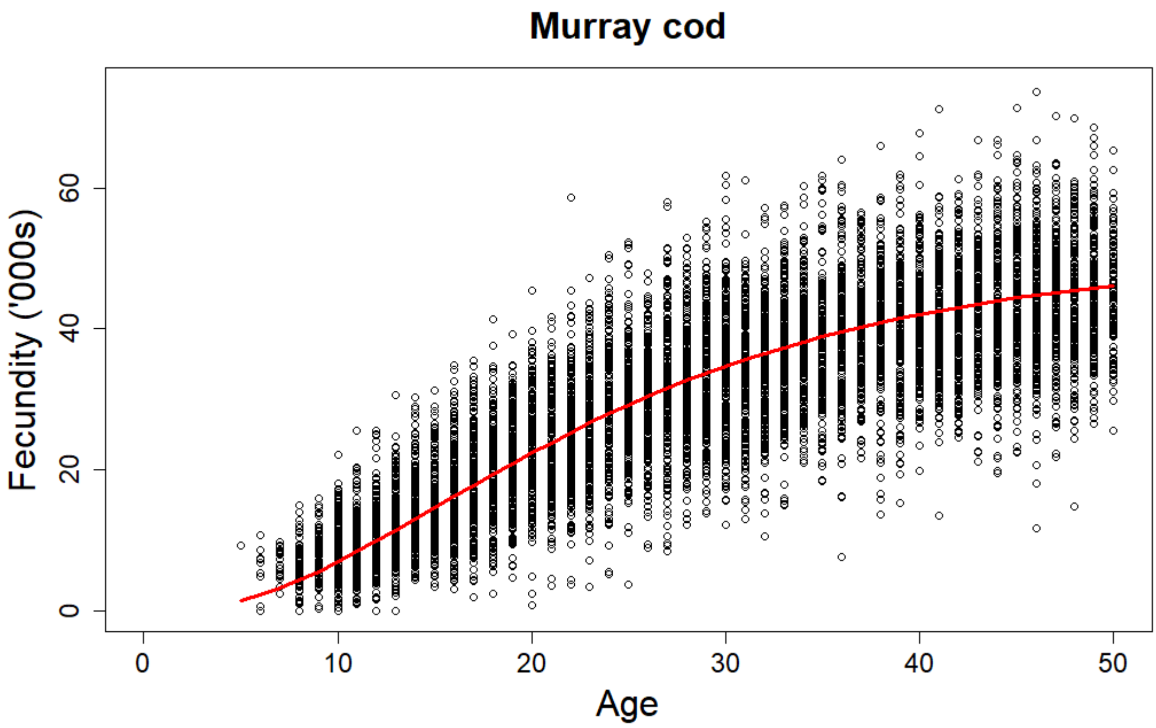


Figure A.2 Age–fecundity used in the population model when the average maximum size of Murray cod is 1200 mm; this relationship is for larger systems such as the Murrumbidgee River

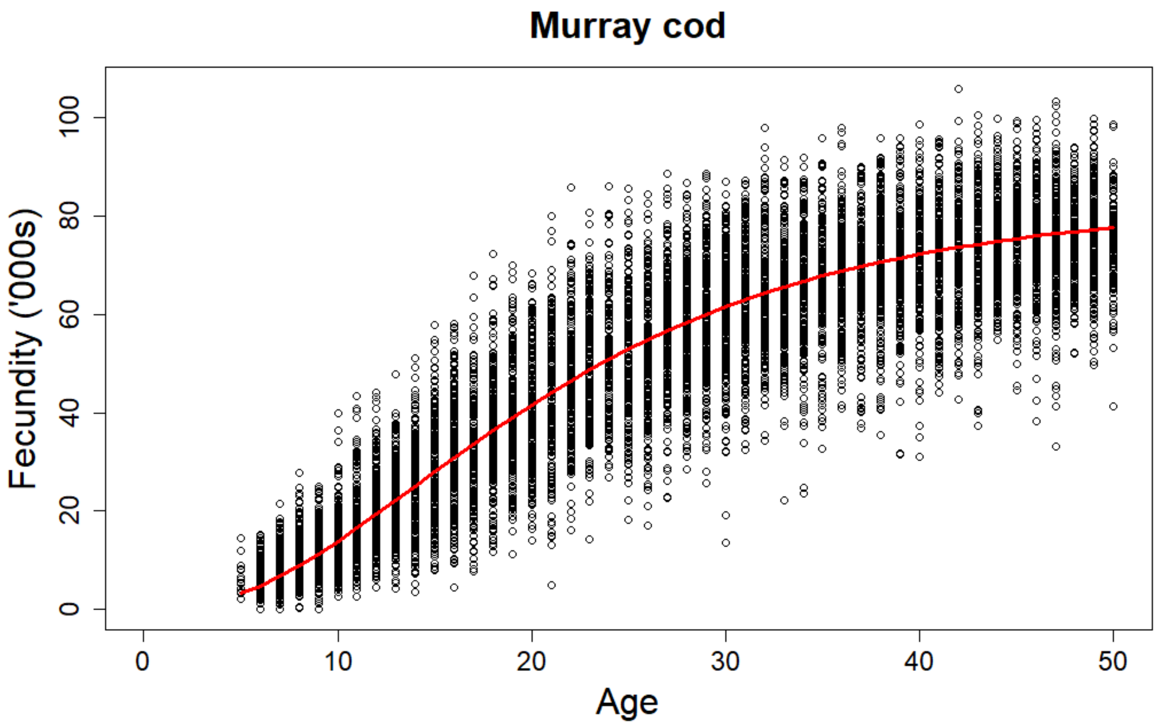


Figure A.3 Age frequency of Murray cod collected in the Basin between 1999 and 2016, with a fitted curve to generate age-specific survival rates

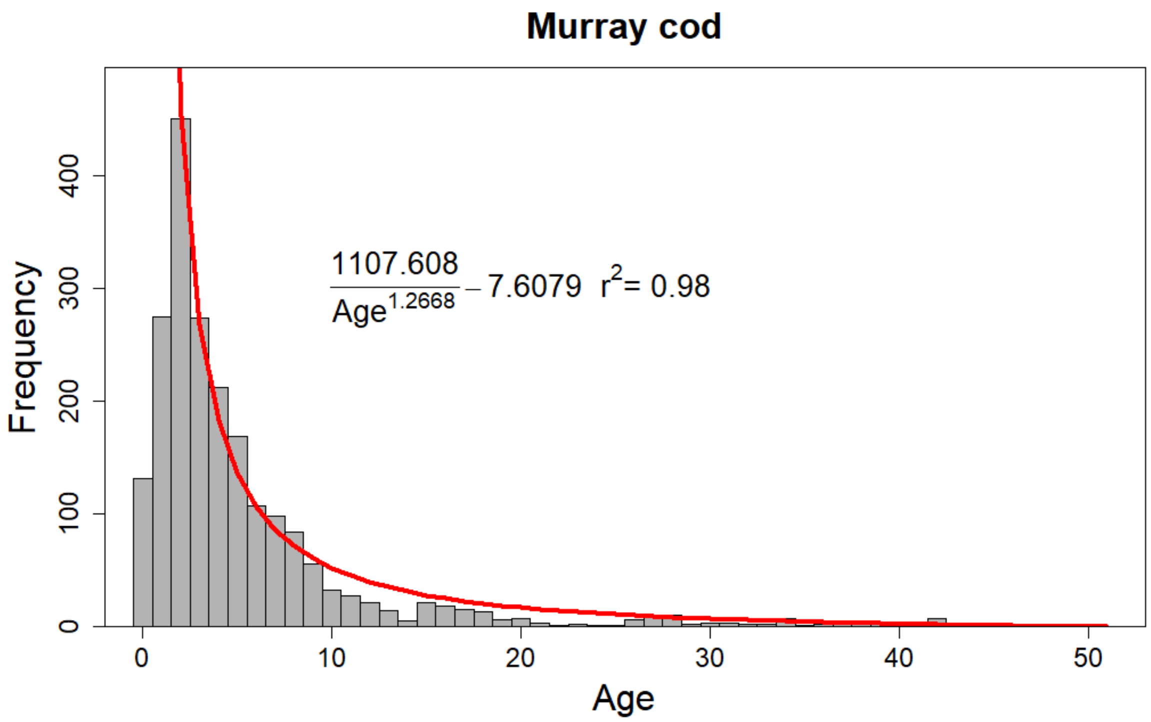
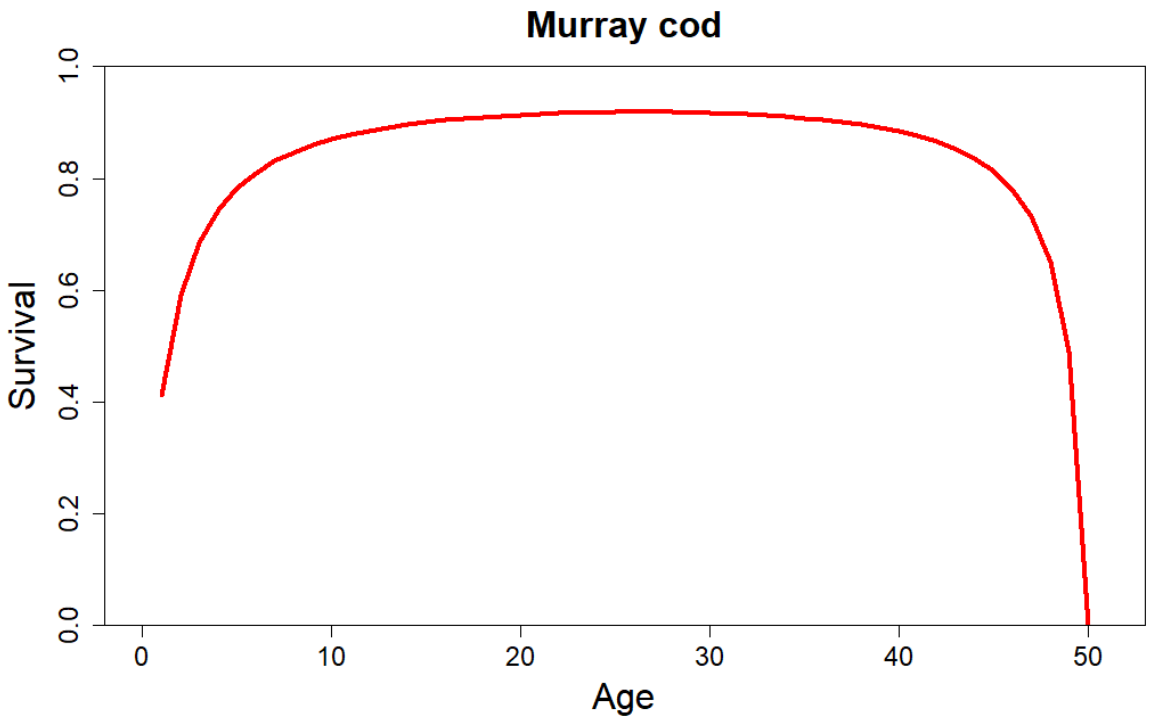


Figure A.4 Age-specific survival rates for Murray cod in the Basin generated from the ratio between age classes of the idealised age frequencies in Figure A.3



Age data obtained by analysing otoliths were used to generate estimates of age-specific survival (Ricker 1975; Todd et al. 2004, 2005; Todd and Lintermans 2015). A total of 1,741 Murray cod were aged from otoliths of fish sampled from the Murray–Darling Basin, collected between 1999 and 2016. An age class can be considered fully represented when the number of fish in the subsequent age class is less than the age class in question (Ricker 1975). The ratio between idealised age classes was taken as the 'average' or mean survival rate (Ricker 1975; Todd et al. 2004; Todd and Lintermans 2015), and see Figure A.3 for the curve generated from which the ratio between age classes provides the estimate of the age-specific survival rate (Figure A.4). Survival rates for eggs, larvae and fingerlings (0+ fish) are unknown, and consequently, as stated in Todd et al. (2005), the rates estimated for the Trout Cod population model (Todd et al. 2004) were assumed to be appropriate for use in a Murray cod population model, eggs ~ 0.5; larvae ~ 0.012 and 0+ fish ~ 0.12.

A.2.2 Murray cod egg and larval survival

Murray cod: 10 days eggs / 10 days as drifting larvae.

Murray cod spawning occurs after 2 days with temperature >18°C.

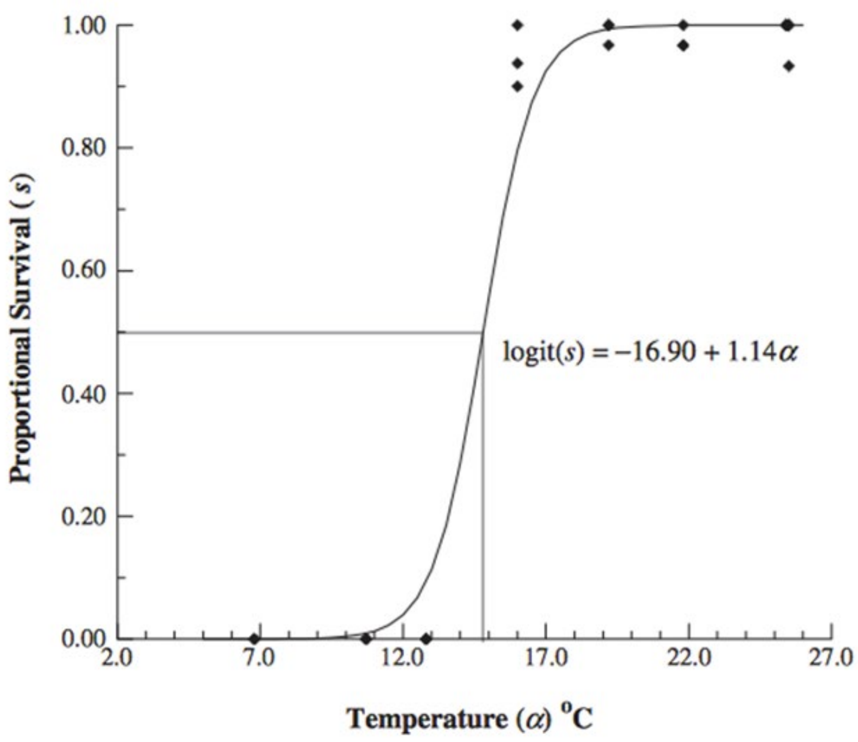
Equation for Murray cod temperature–survival vector (Figure A1.5):

$$daily\ temperature\ effect = \frac{\exp\left(-16.902733 + (temp \times 1.141874)\right)}{1 + \left(\exp\left(-16.902733 + (temp \times 1.141874)\right)\right)}\ ;$$

$$survival = \prod_{i=current\ day}^{20} daily\ temperature\ effect,$$

where the product runs from the current day to the end of the critical egg and drifting larvae period.

Figure A.5 Proportional Murray cod egg and larval survival with increasing temperature



A.2.3 Murray cod initial population size

Table A.1 Murray cod initial population size for the 6 rivers

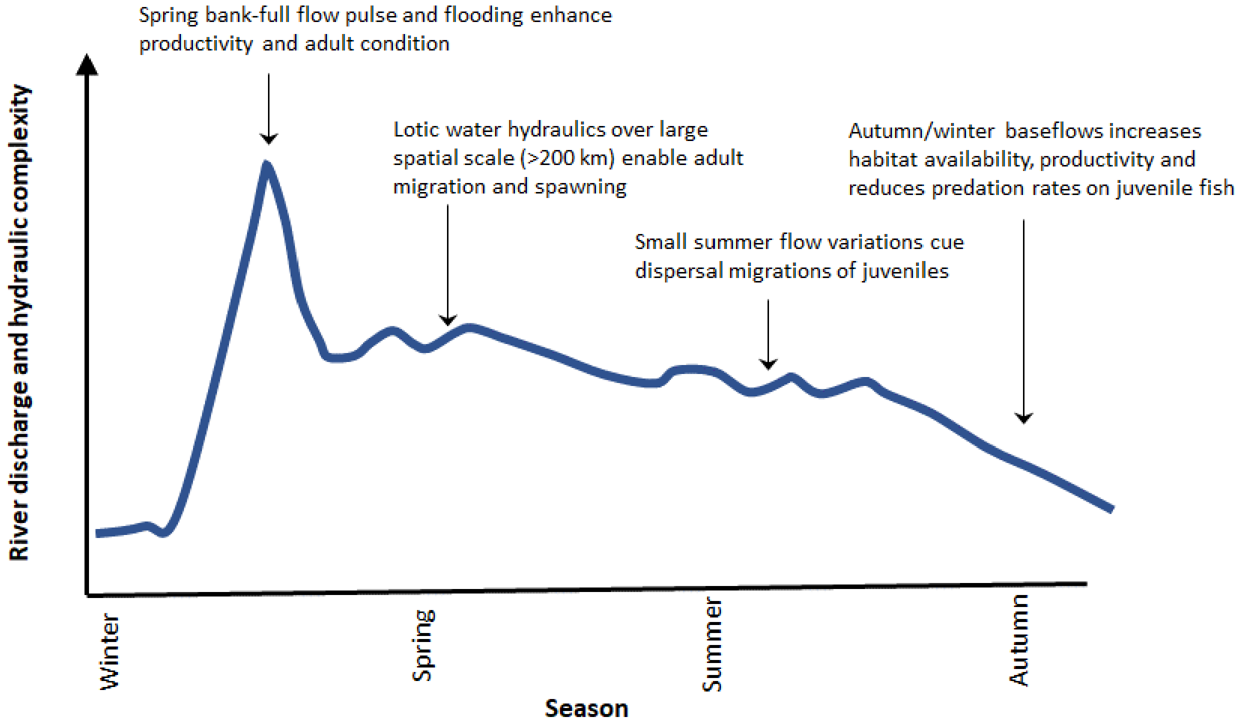
Population no.	River	Initial population size
1	Edward	84,000
2	Goulburn	20,000
3	Gwydir	10,000
4	Lachlan	15,000
5	Murrumbidgee	120,000
6	Lower Murray	200,000

A.3 Golden perch

A.3.1 Golden perch single population construct

Golden perch is a flow-dependent wide-ranging species (Zampatti et al. 2018; Koehn et al. 2020), and in order to capture their life cycle, a stage/age matrix model was constructed to capture the dynamics. A matrix construct was applied to the Murray–Darling Basin sites as a metapopulation model made up of 8 populations, with immigration and emigration between adjoining upstream and downstream populations (Figures A1.7, A1.8, A1.9 and A1.10). This construct came from a number of workshops held as part of the Murray–Darling Basin Authority Fish Population Modelling project, with rules established for all of the linkages based on data (e.g. Mallen-Cooper and Stuart 2003) and expert elicitation (Koehn et al. 2018, 2020). This type of metapopulation for golden perch has previously been used for assessing the persistence of silver perch in the northern Basin (Todd et al. 2022c) and is deemed most suitable for this project. A conceptual model of golden perch life history in relation to important elements of the flow regime also informed the population model construct (Figure A.6).

Figure A.6 A conceptual model of important flow components within an annual flow regime and their relationship to the Golden Perch life history



For each of the populations within the broader Murray and Lower Darling rivers metapopulation, a stage/age matrix model with 4 stages and 30 ages was constructed to represent the life cycle of golden perch: eggs; larvae; juveniles (ages 0–3 years); and adults (ages 4–30 years). Sexual maturity in the model occurs at 4 years of age (Mallen-Cooper and Stuart 2003), and egg production increases with age (Rowland 2005). Both demographic and environmental stochasticity are included in the model. Variation in the survival and reproduction of individuals is modelled by demographic stochasticity (Akçakaya 1991). Demographic stochasticity is incorporated using a binomial distribution to model the number of individuals surviving between consecutive time steps, and a Poisson distribution to model recruitment to the 1-year age class.

Environmental stochasticity is incorporated by randomly varying the survival and fecundity rates each year. Survival rates were drawn from normal distributions transformed to the unit interval (Todd and Ng 2001) with specified means and standard deviations. Age-specific fecundities were determined from a relationship estimated from hatchery data (Rowland 1996) and age–length data with specified means and standard deviations. Todd and Ng (2001) provide a methodology for specifying correlations among survival rates; however, no information exists to quantify these correlations. Given the aquatic habitat in which fish live, it is reasonable to assume that the correlations are likely to be positive and close to unity. We assume that the survival rates perfectly correlate to one another and independent of the fecundity rates; fecundity rates are also assumed to be perfectly correlated with one another (Todd et al. 2004), and a pre-breeding census construction is used (Burgman et al. 1993). The density-dependence construct applies across all age classes. The following equations are for a single golden perch population:

$$FN_{i+1,t+1} = Bin\left(FN_{i,t}, dens_{i,t} \times S_{i,t}\right), \qquad i = 1\ldots 29$$

$$FN_{1,t+1} = Poisson\left(dens_{0,t+1} \times S_{0,t} \times tempeffects_t \times S_{L,t} \times S_{E,t} \times 0.5 \times Eggs_t\right)$$

$$Eggs_t = \sum_{i=4}^{i=30} ST_t \times Fec_{i,t} \times FN_{i,t},$$

$$N_{i,t+1} = 2 \times FN_{i,t+1} \qquad i = 1\ldots 30$$

$$dens_{i,t} = \begin{cases} \exp\left(-ds \times \left(\sum_{i=2}^{i=30} FN_{i,t} \Big/ DT - 1\right)\right), & \text{for } i = 2\ldots 29 \text{ and } \sum_{i=2}^{i=30} FN_{i,t} \geq DT \\ 1, & \text{for } i = 2\ldots 29 \text{ and } \sum_{i=2}^{i=30} FN_{i,t} < DT \end{cases}$$

$$DT = 1.25 \times AFPS$$

$$dens_{1,t} = \begin{cases} \exp\left(-ds_1 \times FN_{1,t}\right) & \text{for } \exp\left(-ds_1 \times FN_{1,t}\right) < 1 \\ 1, & \text{for } \exp\left(-ds_1 \times FN_{1,t}\right) \geq 1 \end{cases}$$

$$dens_{0,t+1} = \begin{cases} \exp\left(-ds_0 \times FN_{0,t+1}^{-d}\right) & \text{for } \exp\left(-ds_0 \times FN_{0,t+1}^{-d}\right) < 1 \\ 1, & \text{for } \exp\left(-ds_0 \times FN_{0,t+1}^{-d}\right) \geq 1 \end{cases}$$

$$FN_{0,t+1}^{-d} = S_{0,t} \times tempeffects_t \times S_{L,t} \times S_{E,t} \times 0.5 \times Eggs_t$$

$$Wei_{i,t} = \exp(W)\left(L_t^{\infty}\left(1 - \exp\left(-K_t\left(i - \mathrm{T}_t\right)\right)\right)\right)^{C_t} \qquad i \geq 4$$

$$W = -12.50$$

$$L_t^{\infty} \sim N(480.48, 6)$$

$$K_t \sim N(0.32, 0.06)$$

$$T_t \sim N(-0.20, 0.3)$$

$$C_t \sim N(3.23, 0.03)$$

$$Fec_{i,t} = P_t \times Wei_{i,t} / 1000 - q\left[Wei_{i,t} / 1000\right]^2 \qquad i \geq 4$$

$$P_t \sim N(249.16, 16.61)$$

$$q = 20000$$

where t is an annual time interval $FN_{i,t}$, and $N_{i,t}$ are the numbers of female adults and total adults, assuming an even sex ratio, in the i_{th} age class at time t; $S_{i,t}$ is a random variate describing environmental variation in the survival rates of golden perch in the i_{th} age class drawn from normal distributions transformed to the unit interval (Todd and Ng 2001) with no loss of information from the specified means and standard deviations; $S_{0,t}$, $S_{l,t}$ and $S_{e,t}$ are random variates describing environmental variation in survival rates of golden perch less than 1 year old, larvae and eggs, respectively (similarly to age-specific survival, where survival rates across all ages and stages are perfectly correlated); $\mathrm{tempeffects}_t$ is the proportional effect of temperature on survival of eggs and larvae (see Todd et al. 2005); $dens_{i,t}$ is the density-dependence factor applied to all age classes; ds and ds_i are the density scale for each location; $EggNum_t$ is the total number of eggs produced at time t; AFPS is the average population size; $Fec_{i,t}$ is the fecundity for golden perch in the i_{th} age class, based on an age–length relationship from 1,347 aged golden perch, a length–weight relationship based on 2,929 golden perch, and a weight–fecundity relationship in Rowland (1996), where age and fecundity are perfectly correlated with each other, but not with survival (see Figure A.7); $Bin(n, s)$ is a random variate representing demographic variation in transition from one age class to the next with a binomial distribution $Bin(n, s) = X \sim \mathrm{Binom}(n, s)$, and $Poisson(m)$ is a random variate representing demographic variation in recruitment with a Poisson distribution $Poisson(m) = X{\sim}\text{Poi}(m)$.

Age data obtained through analysing otoliths from the Murray River were used to generate estimates of age-specific survival (Ricker 1975; Todd et al. 2004, 2005; Todd and Lintermans 2015). A total of 2,968 golden perch were aged from otoliths of fish sampled from the Murray River and catchments and collected over the years 1990 to 2015 (Mallen-Cooper and Stuart 2003; Tonkin et al. 2019). An age class may be considered to be fully represented when the number of fish in the subsequent age class is less than the number of fish in the age class in question (Ricker 1975). The ratio between idealised age classes was taken as the 'average' or mean survival rate (Ricker, 1975; Todd et al. 2004; Todd and Lintermans 2015) (see Figure A.8 for the curve from which the ratio between age classes provides the estimate of the age-specific survival rate in Figure A.9. Survival rates for eggs, larvae and fingerlings (0+ fish) are unknown; consequently, it was assumed that 50% of eggs hatch, and the curve fitted to the age–frequency data was used to estimate larval and fingerling survival at 0.002 and 0.167, respectively, providing a potential population growth rate for golden perch of 1.4.

Figure A.7 Age–fecundity relationship used in the golden perch single population and meta-population model

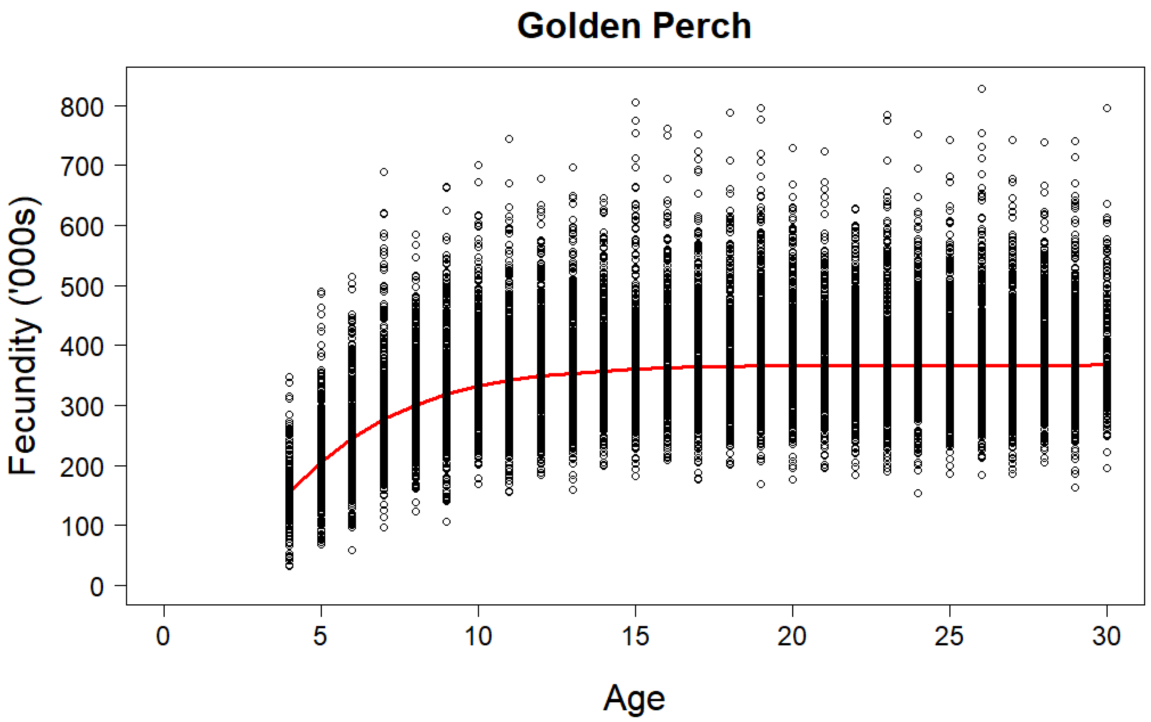


Figure A.8 Age–frequency relationship with the fitted curve used to generate age-specific survival rates for golden perch

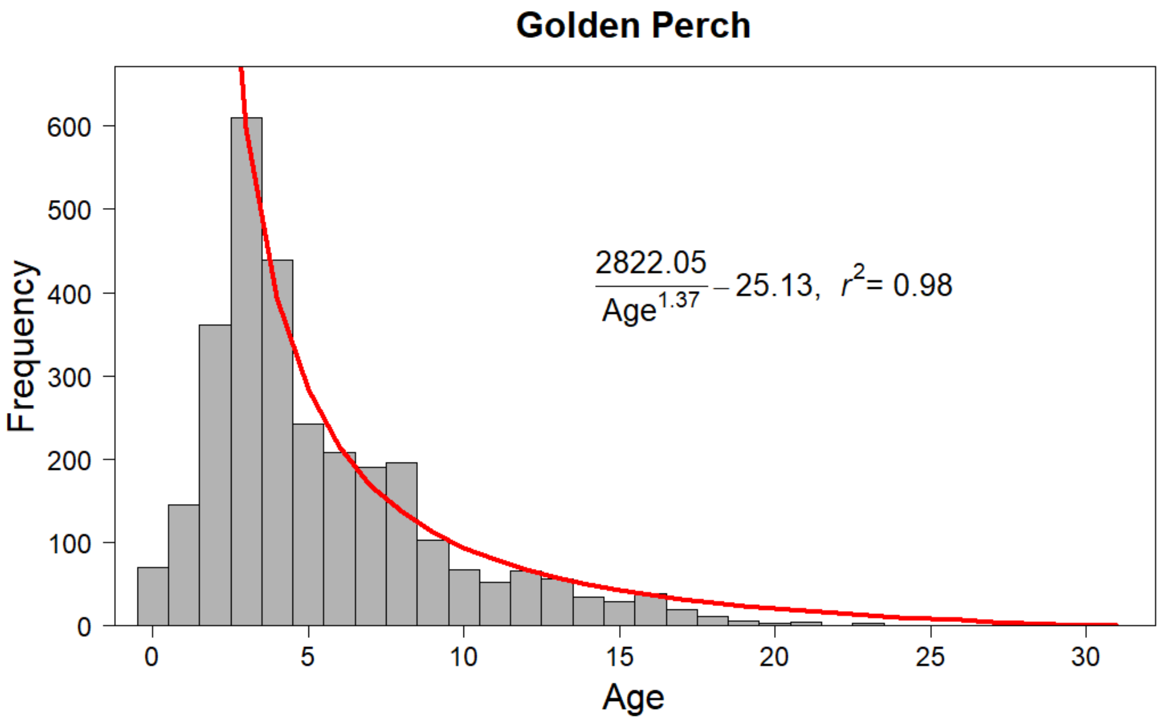
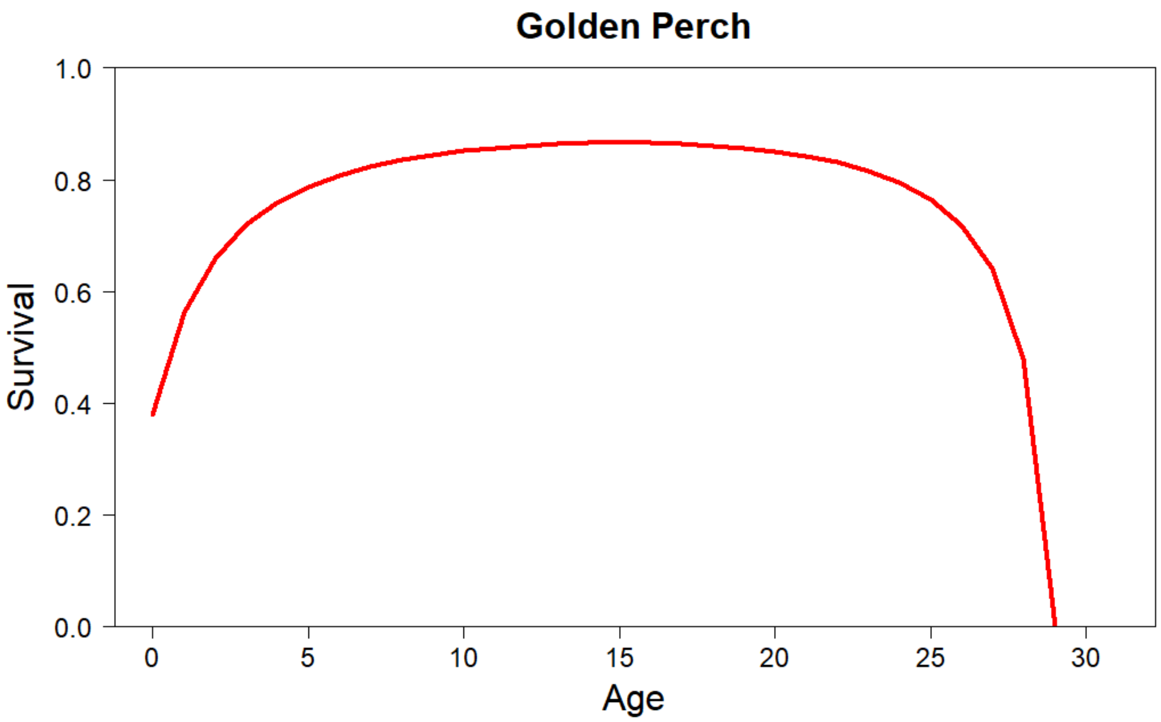


Figure A.9 Age-specific survival rates for Golden Perch generated from the ratio between age classes (from the idealised age frequencies in Figure A.8



A.3.2 Golden perch initial population size

Table A.2 Golden perch initial population size for 14 rivers

Population no.	River	Initial population size
1	Lower Murray	1,000,000
2	Mid Murray	1,000,000
3	Upper Mid Murray	300,000
4	Upper Murray	40,000
5	Lower Darling	800,000
6	Murrumbidgee	200,000
7	Edward	100,000
8	Darling	1,000,000
9	Barwon	1,000,000
10	Gwydir	100,000
11	Warrego	120,000
12	Culgoa	800,000
13	Condamine-Balonne	1,500,000
14	Menindee	0

A.3.3 Golden perch productivity estimation

Productivity was estimated for each modelled year using daily flow records from each reach. Calculations used the following logic:

1. Calculate mean for flows in whole dataset
2. Calculate standard deviation (sd) for flows in whole dataset
3. For each day calculate the Z-Score (subtract mean and divide by standard deviation)
4. Find top 20 Z-Scores for the given year
5. Calculate mean of top 20 Z-Scores for the given year – this is the productivity value for this year

This process can be represented by the following equation:

$$Z_i = \frac{(Flow_i - \mu)}{\sigma}$$

where Z_i is the Z-score on day i, $Flow_i$ is the daily flow in the reach in ML day^{-1} on day i, μ is the mean flow across the whole timeseries of flow data from the reach and σ is the standard deviation of flow data from the reach.

Productivity values were then used to inform early life history (larvae and fingerling) survival of golden perch in each year in model runs.

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