Spatially explicit population models for fish in the Barwon-Darling (Baaka) River

A Report prepared for the Murray Darling Basin Authority

An Australian Government initiative to drive innovative scientific research for the Murray–Darling Basin and its communities.

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CENTRE FOR FRESHWATER ECOSYSTEMS (CFE)
School of Agriculture, Biomedicine and Environment

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Water and Environmental Research Project - Theme 3 Environmental Outcomes

RQ 11.1 Spatially explicit population models for fish in the Barwon-Darling (Baaka) River system

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ENQUIRIES
Luke McPhan
Research Fellow
La Trobe University
Victoria 3086

T 0407 009 320
E l.mcphan@latrobe.edu.au
W latrobe.edu.au/freshwater-ecosystems

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Traditional Owner acknowledgement

La Trobe University proudly acknowledges the Traditional Owners and Custodians of the Country. We pay our respects to the Elders past, present and emerging and respect their cultural heritage, beliefs and relationship with the land, waters and community.

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This work would not have been possible without the contributions of several individuals. Particularly we would like to acknowledge and thank NSW DPI Fisheries for the provision of data that allowed the derivation of fish vital rates in the system in addition to advice and contribution to modelling approaches provided by Jason Thiem and David Crook. We'd also like to acknowledge the assistance provided by Kathrine Danaher (NSW DPI Fisheries) and Gabrielle Hunt (MDBA) in the development of waterhole mapping and persistence analysis via previously collected datasets and advice on the use of remote sensing techniques.

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Executive summary

Since 2018 there has been a sequence of major fish kills in the lower Darling (Baaka) River system that have decimated native fish populations within the local area. These events have deeply impacted local communities and triggered widespread debate regarding the sustainability of current river operations. While the proximate causes of the fish kills have been extensively studied in a series of inquiries and published research, despite much speculation as to the long-term viability of native fish populations in the region, to date there has been a lack of research focused on quantifying longer-term trajectories of populations in this region and or quantitatively assess recovery under potential future scenarios of climate and river management.

To more adequately inform future management planning, estimates of native fish population recovery and potential extinction risks, are required. This includes examining the combined effects of climate change on flow permanence and declining habitat availability, as well as the impacts of local catastrophic fish kills associated with poor water quality, and potential mitigation options such as flow management and increased barrier passage. In this work we develop a spatially explicit dynamic fish population model to assess the population viability of four freshwater fish species (Murray cod, Golden perch, Bony bream and Common carp) of the Darling (Baaka) River under hydrological conditions observed in the past ~40 years. This model combines information on hydrology and waterhole persistence with estimates of fish survival and recruitment to model long-term population trends. By analysing the persistence characteristics of riverine waterholes during cease to flow events and simulating multiple future hydrological conditions we found key drivers of population viability across the Darling (Baaka) River.

Our results show that two large bodied long-lived species, Golden perch and Murray cod, are at risk of local extinction under multiple future scenarios. These model predictions are reinforced by analyses of population age-structure, which shows that average rates of population growth within the system are well below replacement. An absence of the youngest year classes (YOY and 1+ age classes) in high abundance is a notable feature of the Murray cod populations in the Darling (Baaka), particularly upstream of the Main weir at Menindee, and indicates a recruitment bottleneck for the species, limiting population persistence. Given these vital rates and data have been calculated from programs of the past ~30 years, it is unlikely the significant fish kills in recent events (e.g. 2018-19; 2022-23) are the only contributing factor to this problem. Parameterising stochastic population models with these data in addition to comparison of vital rates to populations elsewhere in the Murray Darling Basin for the species show that populations in the Darling (Baaka) are at a high risk of extinction over very short time periods if antecedent cease to flow conditions persist or intensify.

Among the recommendations for future management of the system, flow delivery that aims to alleviate local pressures on populations including prolonged cease to flow events and waterhole turn over would assist in the persistence of populations in the waterholes across the river above the Main weir. Additionally, implementing greater fish passage solutions has been identified as an important step to allow fish dispersal across the system. This would allow dispersal of high density populations of individuals in the river section where these significant fish kill events have occurred, between Weir 32 and the Main weir at Menindee. The Menindee Lakes act as an important nursery habitat for freshwater fish species, and a major source population for the Darling (Baaka) that is largely restricted from contributing to the meta population of the catchment. The metapopulation model supports the contention that barriers at Menindee, and upstream, have a large effect on upstream population sizes. While the population model has thus far only been used to explore a limited range of scenarios, the development of a quantitative tool that can explicitly test the long-term population outcomes of alternative future management scenarios provides an important complement to existing river modelling capability.

Background

Major fish kills that occurred in the summer of 2018-19 (Vertessy et al., 2019) and more recently in early 2023 (Office of the NSW Chief Scientist & Engineer, 2023) in the Darling (Baaka) River system of the Murray Darling Basin, were of a magnitude and severity of clear concern. The event identified a gap in knowledge of the longer-term consequences of a changing climate for fish populations in the region. The Darling (Baaka) River is a dryland river in the Barwon-Darling River system of the Murray Darling Basin and is one of Australia’s most variably flowing rivers (Puckridge et al., 1998). The hydrological characteristics of the Darling (Baaka) River are that of having peak flow conditions during the Austral Spring, often with significant discharge of > 30,000 ML per day and more regular periods where the river channel flows at a low volume occasionally receding into a series of disconnected waterholes. Since 2000 the occurrence of these ‘cease to flow’ events has increased greatly with recent research indicating issues for the system in the form of a reduction in flows and greater frequency of cease to flow periods (Mallen-Cooper & Zampatti, 2020; Sheldon et al., 2022).. As climate change predictions suggest a warmer and drier future, fish kills due to the drier conditions are also likely to be more common. There is an urgent need for increased understanding of how fish populations will respond to predicted change, and to identify and evaluate appropriate management responses. If these conditions persist, we need to understand how any future changes to the duration and frequency of large drying events will impact freshwater fish population stability.

During periods of cease to flow, the river to disconnects into a series of pools, influence the ability of aquatic organisms to migrate and disperse and introduce local ecological drivers that are less influential when the river is connected by flow. While habitat availability, dispersal, community interaction and density dependence effect populations within a waterhole, of significant concern is the increase in waterhole stratification and subsequent turnover causing rapid declines in dissolved oxygen that were attributed to the significant fish kill events of 2018-19 and 2023. Previously the characteristics of waterholes and the development of water resources has been demonstrated to effect populations of fish not only at the waterhole level, but at larger scales, up to the entire riverscape of a catchment (Bond et al., 2015). The influence of dispersal on the persistence of populations across the Darling (Baaka) system is a vector of significant import (Bice et al., 2021; Thiem et al., 2023). This has however been impacted by the introduction of weirs across the system compounding the effects of water development in the system, reducing the magnitude of flows that facilitate reconnection of waterholes and increasing the duration of periods of below historic average flows and cease to flow periods. This connectivity of discreet patches in the riverscape through time in a dynamic system like the Darling (Baaka) River is required for stable populations and is often conceptualised as a ‘meta population’.

Briefly the meta population concept describes local populations across a landscape, in this case a riverscape, are temporally dependent members of a greater collective of local populations (a ‘meta-population’) which is connected or isolated by an environmental vector. In the present case, the annual hydrological characteristics of the Darling (Baaka) River is the environmental factor influencing the meta-populations connectivity. This is how we approached modelling the native fish populations of the Darling Baaka River (Figure 1). Originating at Weir 32 and continuing North-East along the main channel of the Darling Baaka River to the confluence of the Culgoa and the Barwon Rivers the river was divided into a series of sub-populations of 5 km of river distance. This was completed using the Geofabric stream network layer aggregating the “major river” segments of the Darling Baaka River. Where barriers (e.g. weir or regulation structure see Table 1) intersected the river segment, the current river reach was ended at a distance <5 km and a new segment was started measuring 5 km upstream from the point of the barrier. This created a total of 211 sub populations for the meta-population model divided by eight barriers. Additionally, given records of capture of native fish species (provided by NSW DPI) and their importance as a nursery habitat for recruiting native fish species (Sharpe, 2011), the Menindee Lakes were included as sub-populations. To model the individuals in these, fish detections were spatially intersected with the Australian Network of Aquatic Ecosystems (Brooks, 2021) layer in the Lower- Darling (Baaka). This included the following four aggregate lake systems: Lake Cawndilla, Menindee Lake, Lake Pamamaroo and Copi Hollow, Lake Tandure and Lake Wetherell.

Species of interest for these models included bony bream (*Nematalosa erebi*), golden perch (*Macquaria ambigua*), Murray cod (*Maccullochella peelii*) and the silver perch (*Bidyanus bidyanus*). These species are medium to large bodied native fish with lifespans from relatively short lived generally 5-10 years (bony bream) to multidecadal (Murray cod). In the assessment of available datasets and critical information about the populations demographics in the system, silver perch were found to be data poor. This makes the calculation of vital rates for the species, including fecundity and annual mortality and dispersal rate effectively impossible to calculate reliably. Given these limitations, the decision was made to remove the species from this report and bring attention to the need for more knowledge of the species in this system. It is worth mentioning that the low abundances of silver perch are a likely indicator of an unstable population or one at significant risk of perturbation. The impacts modelled for other species in this system would likely extend to Darling (Baaka) River populations of silver perch. Given their pervasive nature and general tolerance to poor water quality, *Cyprinus carpio* was added to this assessment. The species has significant tolerance to hypoxic conditions (Hughes et al., 1983) and recorded behavioural adaptations include aquatic surface respiration to ameliorate the impact of catastrophic events like waterhole turnover and subsequent hypoxia (McNeil, 2004).

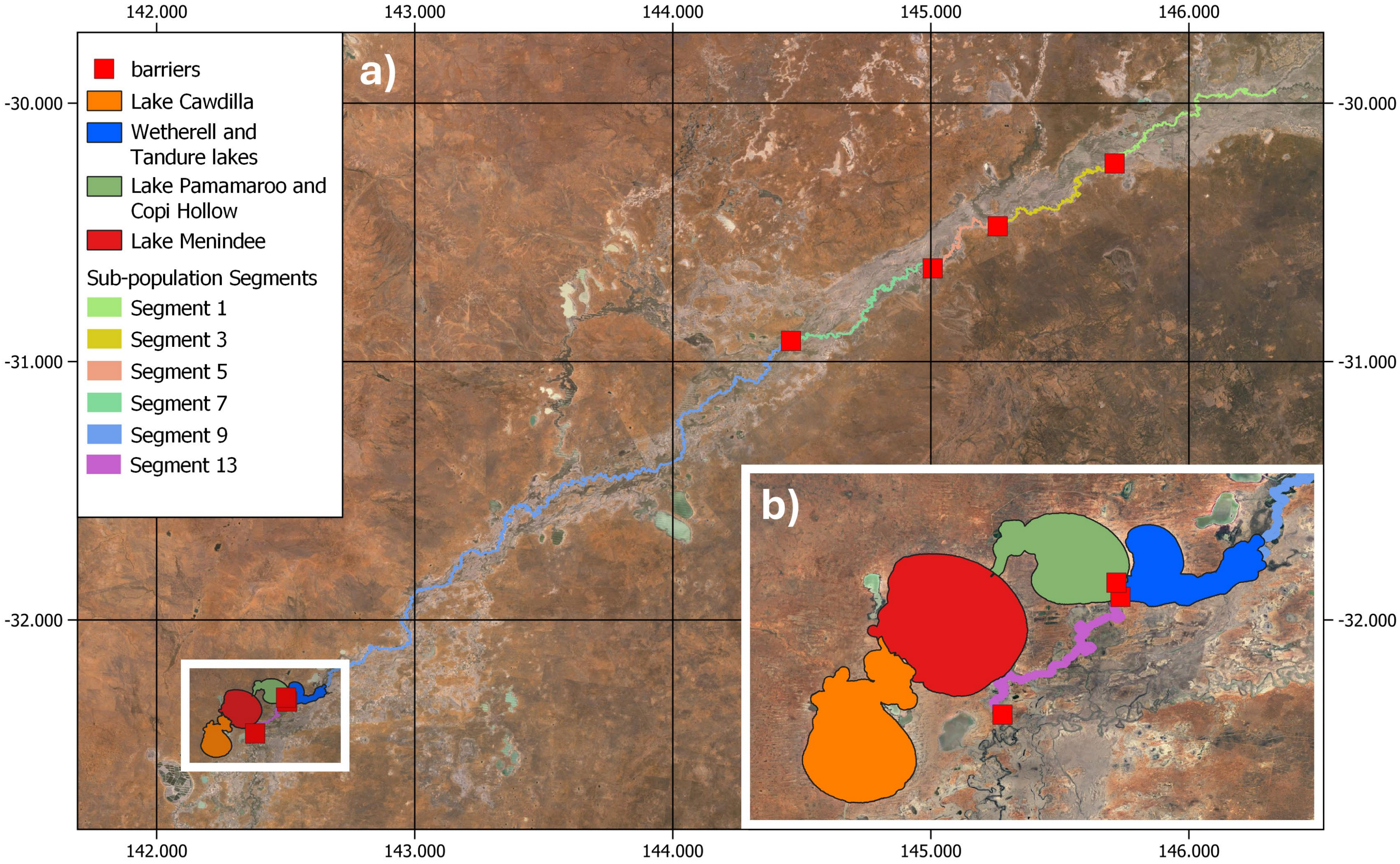

Figure 1. Map of the modelled extents of the Darling showing the a) Entire modelled reach with each reach of sub-population segments shown between barriers (red squares) and b) a close view of the Meinindee lakes system.

Table 1. Barrier details for the modelled area of the Darling (Baaka). Details of each weir include the construction type, height (m) and whether it contains an existing fishway.

Darling Barriers	Type of Weir	Weir Height (m)	Existing Fishway	Passage possible
Tilpa Weir (24)	Fixed Crest	3.3	Yes	Yes
Louth Downstream Weir (21)	Fixed Crest	2.6	Yes	Yes
Louth Upstream Weir (20A)	Fixed Crest	4	Yes	Yes
Bourke Weir (19A)	Fixed Crest	4.4	Yes	Yes
Menindee Storage (Main Weir)	Gated	11.3	No	Downstream
Lake Pamamaroo Inlet Regulator	Gated	10.1	No	Into Lakes
Weir 32 (425012)	-	-	No	No

Introduction to approach

This research focuses on modelling the meta-population dynamics of multiple freshwater fish species significantly impacted by the fish kills in 2018-19 and 2023 by implementing a spatially explicit model of annually varying waterholes in the Darling (Baaka) River. Using field measurements of fish from monitoring programs in the Darling (Baaka) River system we model age-structured populations considering all life history stages and their response to annually varying waterhole hydrologic connectivity. This was to account for the effects of changes to annual carrying capacity in waterholes treating isolated pools during dry periods as components of a meta-population. These meta-population, or matrix population models allow us to predict the population-level outcomes of increasing frequency and duration of low flows and cease-to-flows, including the likelihood and consequences of fish kills under future scenarios of climate and hydrology. Alternative water management scenarios (e.g., environmental flows, variations to flow rules) and mitigation options influencing waterhole persistence can then be evaluated for effectiveness in protecting fish populations in the Darling (Baaka) River system.

The development of matrix population models for modelling fish populations in the Darling (Baaka) River system, reflective of the ecological dynamics requires a developed understanding of multiple factors. To begin understanding antecedent fish populations of the system is a necessity. Within the Risk Analysis and Management Alternatives Software (RAMAS) that we have chosen for this analysis, we investigated the efficacy of using the recently developed RAMAS GIS v6.0 (Akçakaya & Root, 2013); Figure 1) for the fish population models of the Darling (Baaka) system. This program incorporates the spatial dynamics of systems (e.g. inundation extent) into the carrying capacity of individuals in sub-populations across a landscape. These models are reliant on the vital rates of organisms (e.g. mortality, fecundity, migration) to project population abundance across a landscape over time.

Fish survey data from the past ~20 years were made available for the project by NSW DPI Fisheries which included both total catch and demographic information for five species of fish detected in the waterholes of Darling (Baaka) River: *Nematalosa erebi* (Bony bream), *Macquaria ambigua* (Golden perch), *Maccullochella peelii* (Murray cod), *Bidyanus bidyanus* (Silver perch) and *Cyprinus carpio* (Common carp). Additionally, scientific literature that reported population demographics and migratory behaviour for the species were aggregated and used in combination with the aforementioned data to calculate demographic population parameters. We next modelled the available habitat for fish in reaches of the river. Again, NSW Fisheries were able to provide surveyed waterhole depths and areas associated with multiple surveys during cease to flow periods. We combined these data with an analysis of annual hydrology and inundation extent via remote sensing to identify waterholes in the landscape and analyse waterhole persistence during cease to flow events of varying duration from the past ~40 years. In doing this we modelled the volume and available wet area habitat across the Darling (Baaka) system including the Menindee lakes.

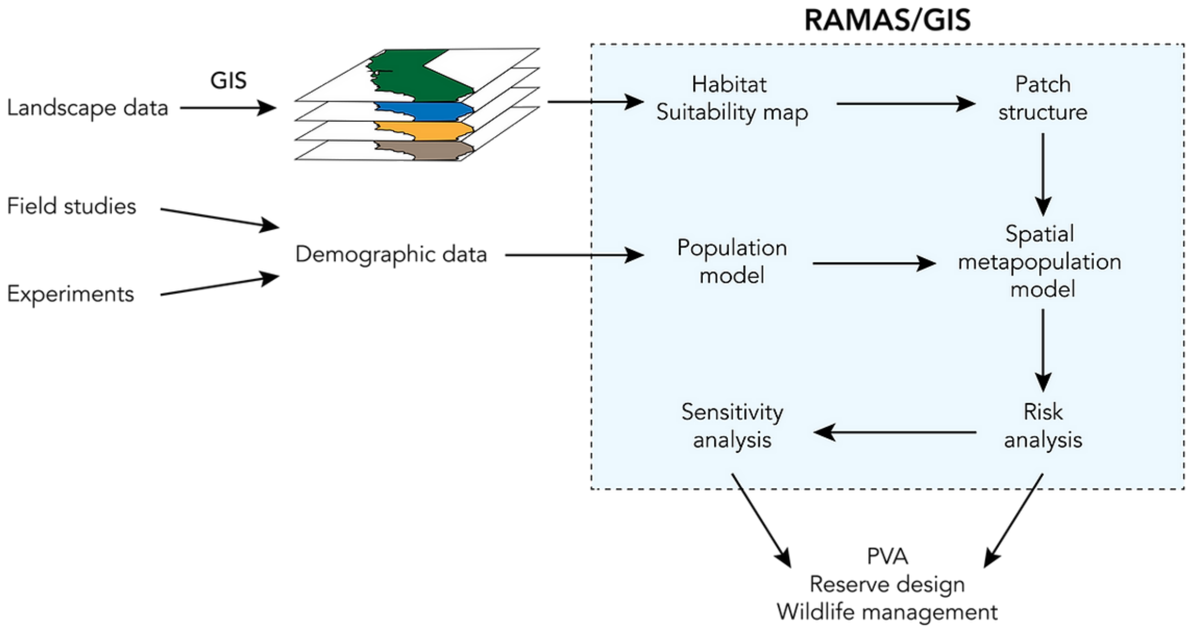

Figure 2.Workflow for RAMAS GIS v6 showing the data sources for model parameterisation on the left and side (Landscape data, field studies and Experiments), and how they contribute to the workflow of RAMAS GIS. In the blue box on the right had side first the processing of landscape data into Habitat suitability and patch structure is completed as a contribution to Spatial metapopulation models, and demographic data is used to generate the parameters of the population model which generate a meta population model of organisms. Subsequently this model can be analysed via Risk factors of extinction and population size are returned and can be analysed via Sensitivity analyses and contribute to a greater understanding of population viability. Source (https://www.ramas.com/gis-6-0)

Given recent conditions and predicted future hydrological trends for the Darling (Baaka) River, the system will likely be characterised by a drier hydroclimate with greater variability. There are however some global climate models predict an increase in wet conditions and thus we must consider alternative futures (Department of Environment Land Water and Planning et al., 2020). In addition to climatic drivers of population persistence, local drivers of population dynamics and fish kill events occur at the sub-population level. Under prolonged periods of disconnection, physicochemical parameters (e.g. temperature, dissolved oxygen, salinity) of individual waterholes of sufficient depth will vertically stratify. Of significant note is the vertical stratification of dissolved oxygen in these waterholes. Within a waterhole organic matter sinks to the benthos over time and contributes to an increased gradient in dissolved oxygen via bacterial respiration. Where vertical gradients are low and both air and water surface temperatures have low variability, waterhole inversion or turnover has a very low likelihood, though when vertical gradients are high, the likelihood of waterhole turnover increases and when realised can have significant ecological impact (Vertessy et al., 2019).

To incorporate this into our assessment of fish populations in the Darling (Baaka) River we opted to use a decision-scaling framework given some uncertainty in the data sources being used to develop hydrological scenario’s (Brown et al., 2012; Brown et al., 2019; Poff et al., 2016). Two contributing factors to fish kills were included in this: hydrological conditions influencing cease to flow event duration, and waterhole turnover likelihood and subsequent hypoxia as a “catastrophic stochastic” process in our population models. This leads to our final analysis of outputs from our fish population models constructed in RAMAS Metapop v6, (Akçakaya & Root, 2013), and an assessment of population stability and viability under changing environmental conditions.

Methods and Results

FISH VITAL RATE DERIVATION

Catch information for focal species; bony bream (*Nematalosa erebi*), golden perch (*Macquaria ambigua*), Murray cod (*Maccullochella peelii*) and common carp (*Cyprinus carpio*) were aggregated from five monitoring programs targeting native and introduced freshwater fish in the Darling (Baaka) River (Figure 2). Survey data that was provided by NSW DPI Fisheries was aggregated across several monitoring programs undertaken in the catchment. Captures of target species of fish from the following programs were included in the calculation of age frequency and CPUE of individuals:

- Basin Plan Environmental Outcomes Monitoring (2015-2020),
- Integrated Fish Monitoring - Murray Darling (2004-2012),
- Murray-Darling Basin Fish Surveys (2015-2022),
- NSW Rivers Survey (1994-1999),
- Sustainable Rivers Audit (2005-2012).

Three of the species (*Cyprinus carpio, Macquaria ambigua and Nematalosa erebi*) showed expected length frequency distributions with the highest abundances of smaller recruiting/juvenile individuals and a gradual decline in frequency with body size. However, whilst this trend for greater juvenile individuals was similar for *Macullochella peelii*, the lower abundance of individuals than other species caused more noise in this relationship.

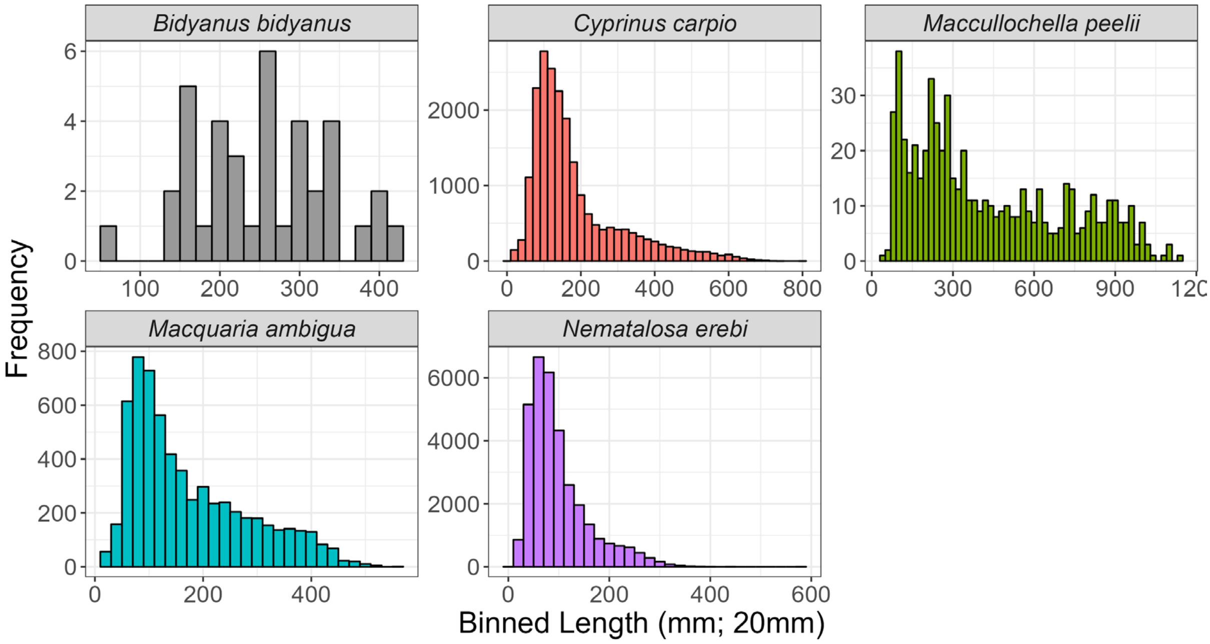

Figure 3. Size frequency of focal species. Fish were binned into 20mm length classes and their frequency aggregated across all programs.

Continuing analysis on the four species of interest (with silver perch removed), survey methods were restricted to boat electrofishing and fyke net catches to generate a standard effort, i.e. catch per unit effort (CPUE), across monitoring programs. The CPUE was calculated as the total catch of each species for each operation (one sampling unit, i.e. net or electrofishing shot) divided by the hours of net soak time in the case of fyke nets and the minutes of electrofishing in the case of boat electrofishing (*sensu* SRA standard methods; Davies et al. (2008)). In this way CPUE was calculated for the four species in each operation across the programs.

Age-Length relationships

Species specific age structure is required for modelling populations in a detailed manner. Contemporary age-length relationships were unavailable for all species, particularly for populations in this section of the Darling (Baaka) River. There are generally two approached to developing these relationships. First, and preferrable, is to model an age-length key (ALK) producing likelihoods of age from length given a training dataset of age verified individuals (e.g. via otolith microstructure analysis). Second, the use of Von Bertalanffy growth estimates can provide length at age information in a similar manner though incorporates less growth variability across individuals into calculation of age. Following the approach of previous studies (see Wright et al. (2020) for *Macquaria ambigua*) we derived relationships that take the form of ALK's. Otolith data made available from other work completed by the QLD Department of Environmental Services was used to generate ALK's for the fish in the Darling (Baaka) system. This dataset included three of the species of interest including 175 otoliths from bony bream, 324 from golden perch and 114 from common carp. These otoliths had been sectioned and annual increments (age) recorded for each individual with length at capture (mm). From these data models are built using a multinomial modelling approach where a log logistic regression of length predicted by age is completed for each age class (Figure 4).

Additionally, given the lack of otolith information available for Murray cod, ages were calculated for all species, from Von Bertalanffy growth estimates of length at age. These were taken from multiple sources and the values for each parameter were collected to generate these growth curves (Figure 6). This type of growth curve takes the form of:

$$L(t) = L_{\infty}\left(1 - e^{-k(t-t_0)}\right) \tag{1}$$

where L(t) is the length of an individual at age t, L_{∞} is the asymptotic or theoretical maximum length of the species, t_0 is the theoretical time at which length is 0 and k is a growth rate parameter of the species across their life history. Our interest in the use of this equation was to invert it algebraically to determine the age (t) of an individual given its length. After manipulation the equation we used took the form:

$$t = \frac{\ln\left(1 - \frac{L_{(t)}}{L_{\infty}}\right)}{-k} + t_0 \tag{2}$$

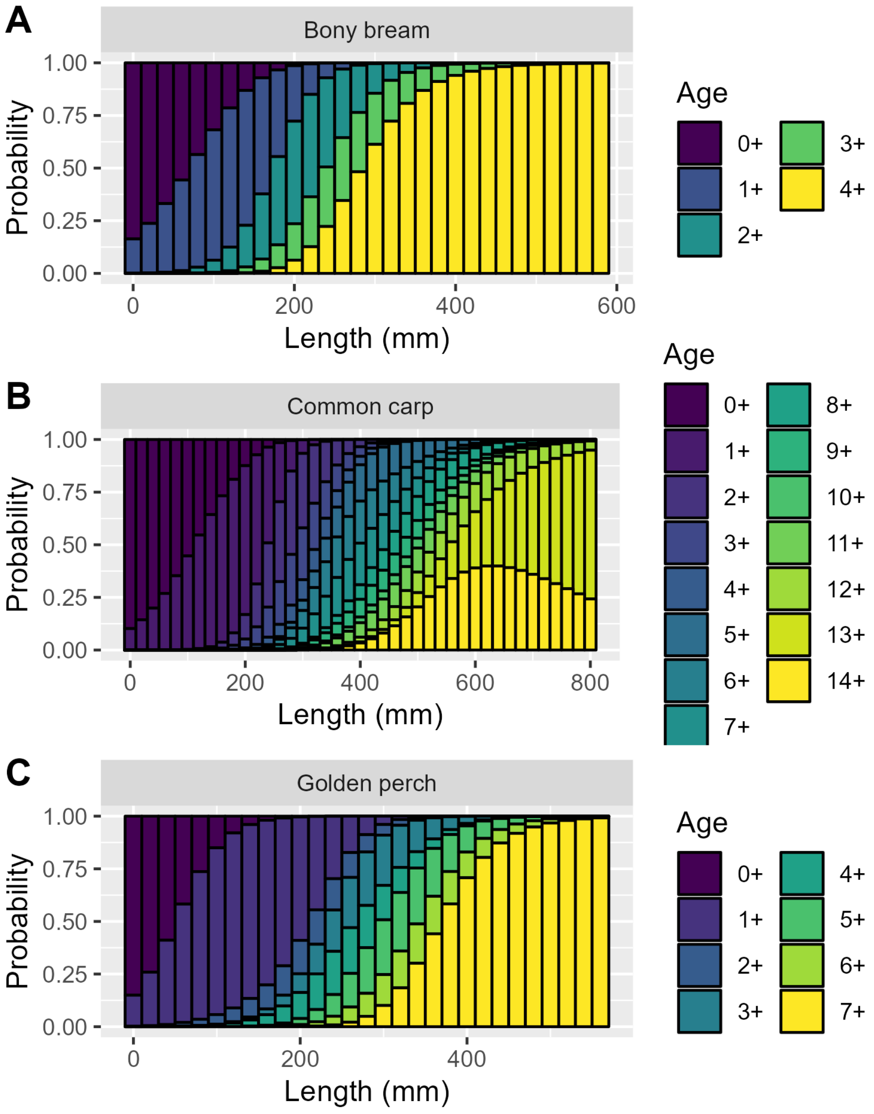

Figure 4. Age Length Keys for A) Bony bream, B) Common carp, C) Golden perch showing for lengths bins of 20mm the likelihood of existing within any specific age group

While this approach gives a determined age for a given length, there is less variability incorporated into the estimates than the ALK's we described above, these curves (Figure 7) were available for all species and their use is common practice in fish biology research.

Age frequency and community composition

Across the five monitoring programs for each species the aggregated CPUE was calculated (Table 2) in addition to the proportional CPUE using a method outlined by Balcombe et al. (2006). Here the proportional abundance (CPUE) of a measured community is used to reflect member composition. We calculated the most abundant species on average across programs was *Nematalosa erebi* accounting for 56.8% of the individuals measured across programs, followed by *Cyprinus carpio* (23.6%), then *Macquaria ambigua* (6.4%) and *Maccullochella peelii* (1.2 %). From these data individuals had been measured for total length (*Macullochella peelii*, *Macquaria ambigua*) or fork length (*Cyprinus* *carpio, Nematalosa erebi*) allowing the calculation of age distributions from Von-Bertalanffy growth curves (Figure 5). This was completed to gain an understanding of the age structure of CPUE across the populations of each species and subsequently used to calculate demographic rates of mortality and fecundity for each species. We calculated the age frequency of the population (Equation 2, Figure 6) and aggregated the ages greater than the 95th percentile into a single age class for future stage structured parts of the analysis. This created age classes from 0+ to 4+ for *Nematalosa erebi*, 6+ for *Cyprinus carpio*, 8+ for *Macquaria ambigua*, and 11+ for *Macullochella peelii*.

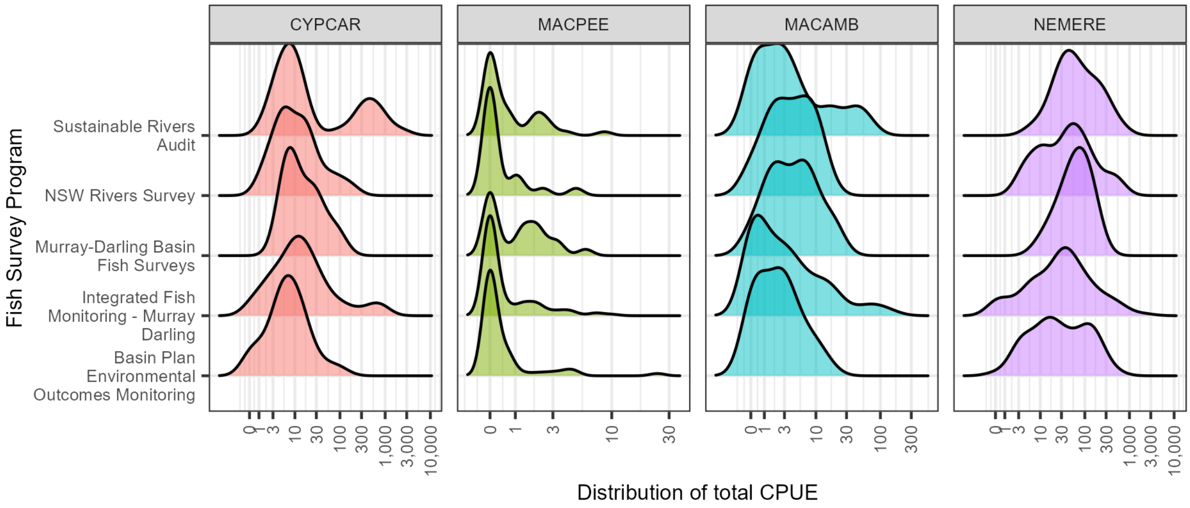

Figure 5.CPUE distribution across monitoring programs for each species of interest (species shown as abreviated species names CYPCAR = Cyprinus carpio; MACAMB = Macquaria ambigua; MACPEE = Maccullochella peelii; NEMERE = Nematalosa erebi)

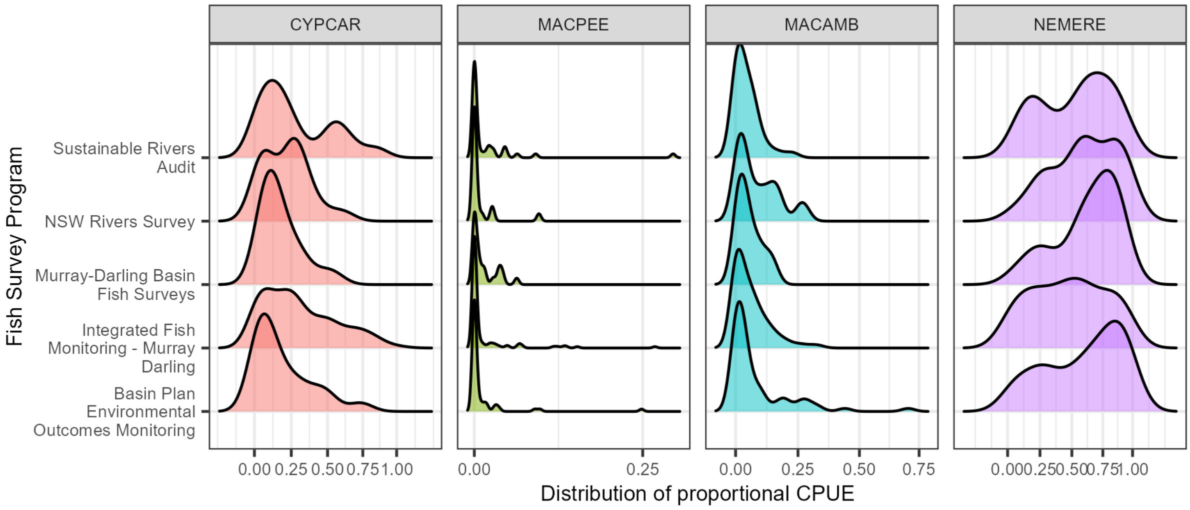

Figure 6. Proportional CPUE distribution across monitoring programs for each species of interest (species shown as abreviated species names CYPCAR = Cyprinus carpio; MACAMB = Macquaria ambigua; MACPEE = Maccullochella peelii; NEMERE = Nematalosa erebi)

Table 2. CPUE for the four focal species measured across 5 monitoring programs as part of the surveyed community of fish. Shown as a) aggregated mean CPUE across the program and b) as the mean proportion of the whole community.

CPUE measure	**Program**	***Cyprinus carpio***	***Macquaria ambigua***	***Maccullochella peelii***	***Nematalosa erebi***
a) Total CPUE	Basin Plan Environmental Outcomes Monitoring	12.52 (19.57)	3.13 (3.57)	0.83 (3.14)	65.89 (90.35)
	Integrated Fish Monitoring - Murray Darling	68.39 (178.38)	9.61 (22.91)	0.78 (1.67)	102.14 (250.34)
	Murray-Darling Basin Fish Surveys	23.32 (25.73)	5.86 (5.65)	1.27 (1.52)	76.21 (50.88)
	NSW Rivers Survey	22.76 (37.25)	4.93 (4.01)	0.52 (1.21)	89.26 (134.41)
	Sustainable Rivers Audit	199.14 (428.69)	9.51 (16.02)	0.92 (1.65)	116.07 (138.76)
b) Proportional CPUE	Basin Plan Environmental Outcomes Monitoring	0.19 (0.2)	0.08 (0.13)	0.01 (0.04)	0.6 (0.31)
	Integrated Fish Monitoring - Murray Darling	0.31 (0.25)	0.06 (0.07)	0.01 (0.04)	0.48 (0.29)
	Murray-Darling Basin Fish Surveys	0.18 (0.14)	0.05 (0.05)	0.01 (0.02)	0.62 (0.25)
	NSW Rivers Survey	0.22 (0.16)	0.09 (0.08)	0.01 (0.02)	0.61 (0.26)
	Sustainable Rivers Audit	0.28 (0.25)	0.04 (0.05)	0.02 (0.05)	0.53 (0.28)

Table 3. Von-Bertalanfy parameters for modelled species and where they were sourced.

Species	L_∞	k	t_0	Source
Bony herring	375	0.29	-0.98	Arriagada (2022)
Common carp	688	0.35	-0.17	Vilizzi and Walker (1999)
Golden perch	439	0.34	-0.49	Wright et al. (2020)
Murray cod	1360	0.067	-1.54	Koehn et al. (2020)

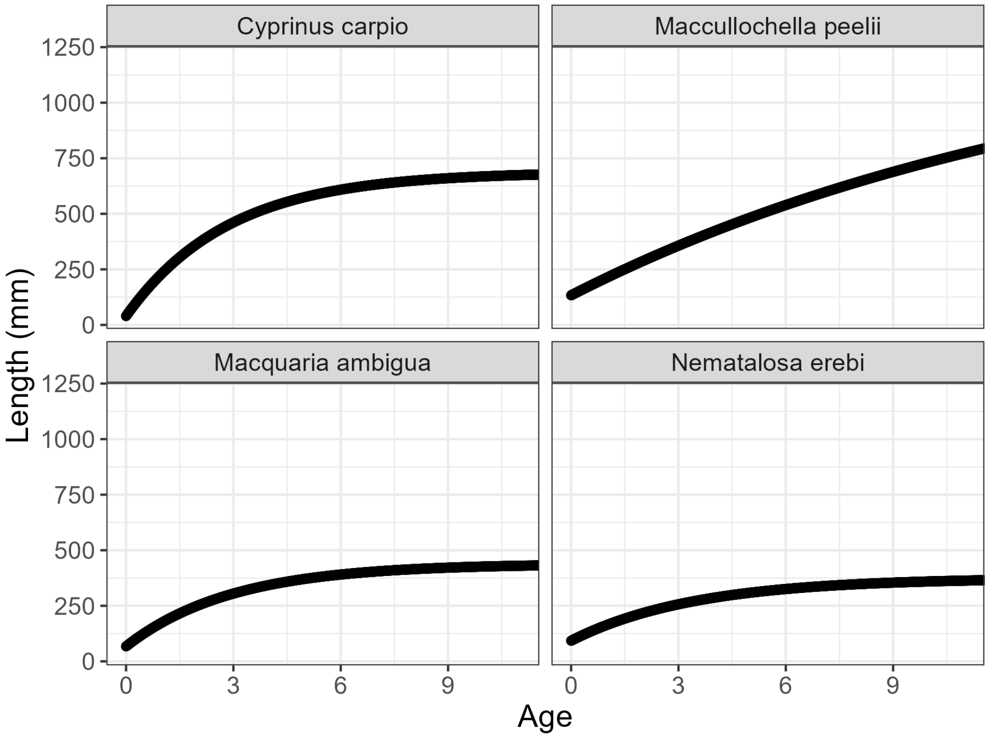

Figure 7.Von-Bertalanfy growth curves for each focal species.

Annual mortality

We used an approach to calculating mortality outlined by Ogle (2018) involving the analysis of a catch curve across an age structured population. Using the age frequency calculated previously, the CPUE for each operation across programs was recalculated for each age class to determine the mean age structured CPUE. After this a log-linear regression was calculated across ages above the most frequent CPUE (“Dome” Figure 9). Given we had truncated the age classes for the > 95th percentile individuals the oldest age class was left out of this analysis to avoid the influence of the aggregated values in this final age class on the linear fit.

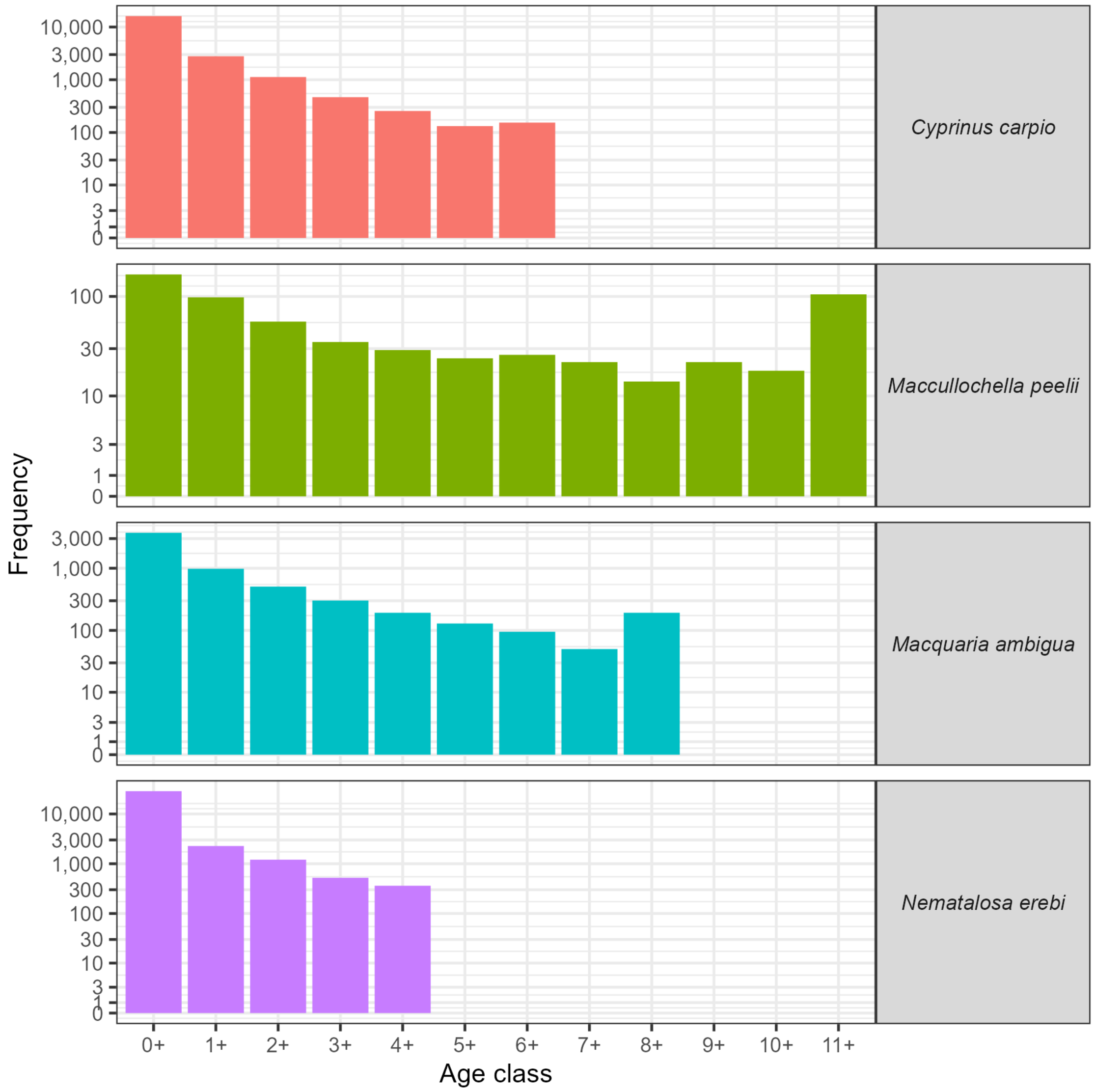

Figure 8. Age frequency of focal species. Frequency of occurrence of each age class for species shown on a log scale.

In calculating rates of mortality for fish of the Darling (Baaka) system we needed to account for the fact that significant hydrological impacts on fish populations occurred across our data (e.g. 2018-19 Fish kill event; Vertessy et al. (2019)). To do this, the interannual variability in mortality, though also fecundity, was incorporated into our catch curve calculations via a random slope for each hydrological year (April to March) included in the final dataset. Years where there were less than 3 age classes represented across the catch were removed from this analysis. This allowed catch curve slopes, and subsequently annual mortality estimates, to vary annually and between programs. Because fish were not always sexed during these surveys, male and female growth and survival rates were presumed equal in this analysis.

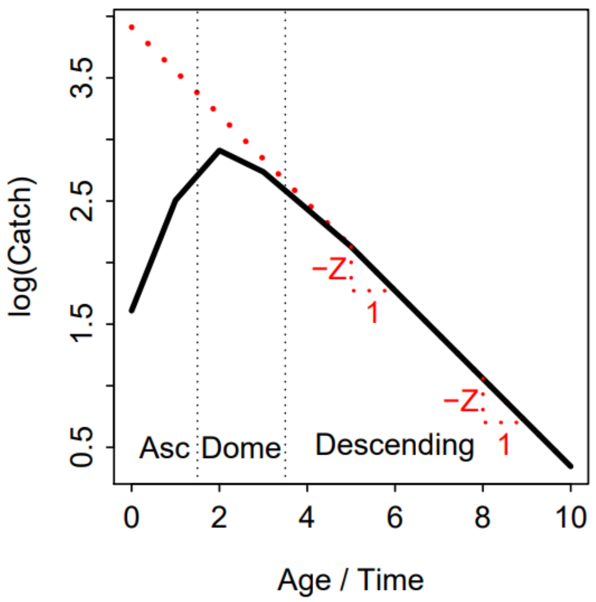

Figure 9. Conceptual figure taken from Ogle, 2018 showing the "descending" limb to calculate the mortality of a population upon which a catch curve of mortality (Z) can be calculated.

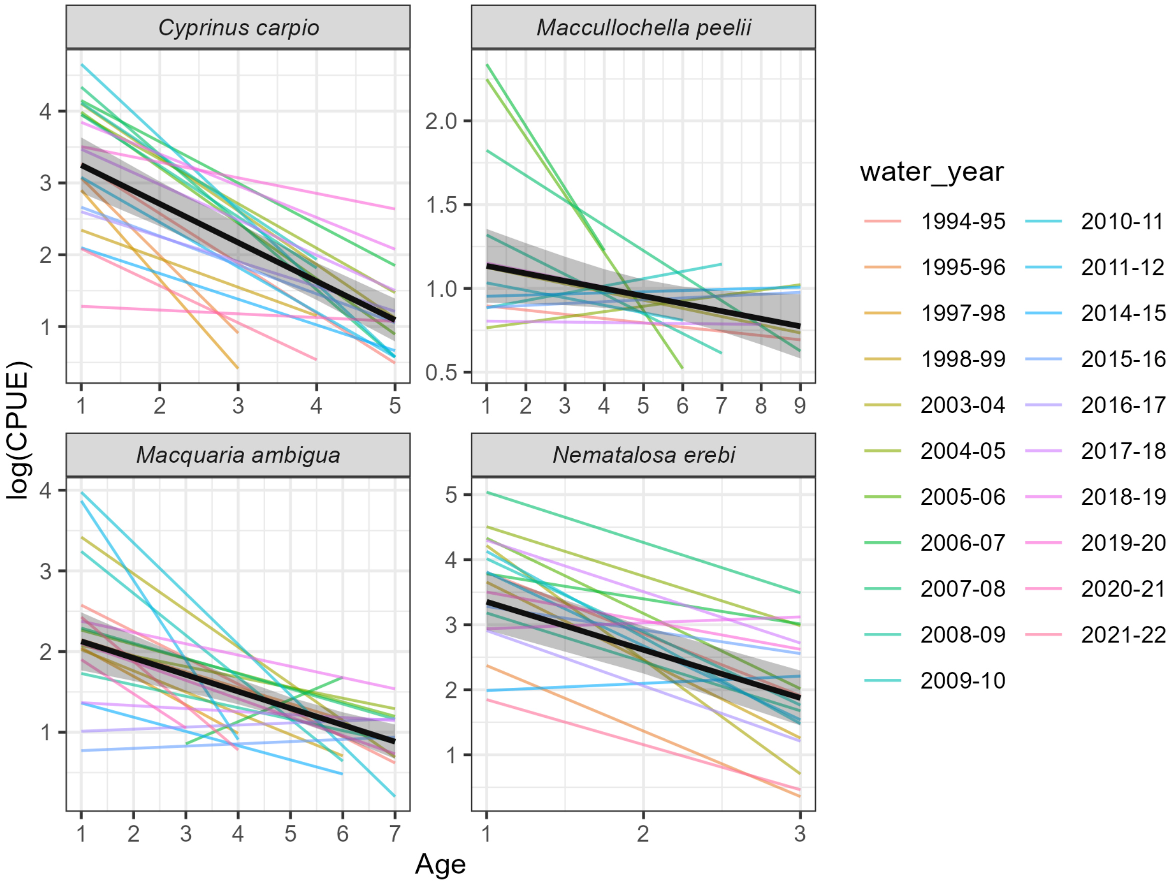

Figure 10. Catch curves with annual variation in slopes, mean relationship between log(CPUE) and age shown in black with 95% confidence in slope.

Carrying capacity and initial conditions

Prior to the calculation of initial abundances and stage structure the abundances of the carrying capacity Initial abundances were begun at 80% of the maximum carrying capacity per waterhole. However, to avoid any bias associated with these initial conditions, the first ten years were removed from these models and treated as a burn-in period when running the models and ignored in the results. Using the maximum stocking rates for farm dams as in Boyd (2006) of ~0.05 fish per m^2 as a carrying capacity for golden perch (*sensu* Bond et al. (2015)), we used the proportional CPUE metric calculated above to generate the likely densities of other species. Given their proportional CPUE, the relative densities were 0.617 fish per m^2 for *Nematalosa erebi,* 0.405 fish per m^2 for *Nematalosa erebi, and* 0.007 fish per m^2 for *Macullochella peelii*. These rates were calculated to easily translate the wetted area within a reach to its maximum carrying capacity.

Fecundity

The fecundity of species was determined as the proportion of spawned individuals surviving to recruitment (a 0+ individual). This metric was calculated by dividing the CPUE of 0+ individuals in the current year by the abundance of mature adults in the year prior. This generated a mean fecundity for *N. erebi* of 7.64 individuals per adult (CI 95 [0.05 : 69.6]), 23.5 individuals per adult for *C. carpio* (CI 95 [0.17 : 152]), 1.5 individuals per adult for *M. ambigua* (CI 95 [0.118 : 5.7]) and 0.255 individuals per adult *M. peelii* (CI 95 [0.05 : 0.915]).

Given vital rates calculated from demographic data were close to or below replacement (i.e. fecundity approx. or < 1) for Golden perch and Murray cod, the demographic data for these species were sourced from Yen et al. (2013) and Todd et al. (2005) prior to modelling these species. Vital rates for populations of Bony bream and Common carp had replacement rates (Fecundity ~ Total mortality) that supported populations and the vital rates from catches of these species in the Darling (Baaka) were used in population modelling. Because fish were not always sexed during these surveys, male and female growth and survival rates were presumed equal in this analysis.

Dispersal

Given we modelled the movement of species between years for the purpose of breeding and colonisation in sub-populations, the most important consideration was the migration of species between these locations as opposed to ‘behavioural movements’ centred around a home range. While there are many studies that monitor movement within a season for most of the focal species, particularly for *M. ambigua*, there were none that could be used to parameterise *N. erebi* dispersal. Given this lack of information for *N. erebi* and both the broad distribution and significant proportional of both this species and *C. carpio*, individuals of these species were given an equal likelihood of migrating or remaining in the current waterhole each year. After this the proportion of individuals dispersing (50%) to any waterhole without passing a barrier was 0.35 and then remaining 0.15 was split between reaches downstream (10%) and upstream (5%) of passable barriers (i.e. those that have fishways).

For *M. ambigua* and *M. peelii*, dispersal kernels of exponential decay with distance were calculated for the proportion of individuals to any other waterhole. This was calculated using the following formula:

$$\begin{aligned} M_{ij} &= a^{\left(\frac{-D_{ij}^{c}}{b}\right)}, \qquad && if\ D \leq D_{max} \\ M_{ij} &= 0, && if\ D > D_{max} \end{aligned} \tag{4}$$

Where M_{ij} is the proportion of individuals dispersing between two waterholes (i and j), and the other parameters were as follows for each species: *M. ambigua* (a = 0.6, b = 20, c = 1, D_{max} = 80) and for *M. peelii* (a = 0.6, b = 10, c = 1, D_{max} = 70). The dispersal proportions from this formula (Figure 9) were calculated pairwise for each waterhole in the landscape and if these coincided with a barrier the proportion passing the barrier was halved. For example, if two waterholes, *i* and *j* were separated by 10 km ~5% of *M. peelii* individuals would migrate from *i* to *j*. However if there was a barrier with a fishway between these locations the proportion migrating would be 2.5%. This was based on reported passage rates through fishways in previous literature being ~50% (Bice et al., 2021).

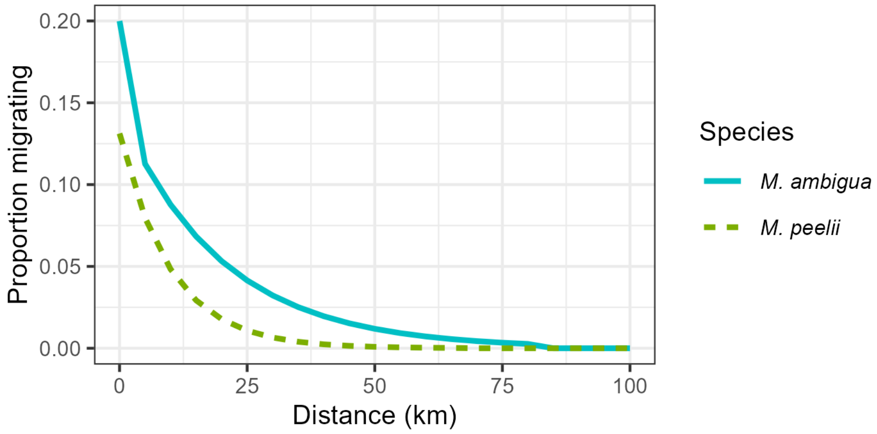

Figure 11. Dispersal kernels for M. ambigua and M. peelii showing the proportion of individuals that move between 2 waterholes separated by a certain distance (Km).

While these rates are calculated on published information for species (Bond et al., 2015) or simply assumed as even distributions and movement across the catchment, there is need to incorporate local contemporary information about the movement of species in future models. As an example, tagged individuals over a two year study of *M. ambigua* movements of individuals upstream of the Wilcannia weir resulted in a net upstream displacement of a moderate number of individuals >500km and up to 1500Km (unpublished data Thiem and Ryan, 2023). Due to limitations imposed by the selected software, RAMAS Metapop v6, modifying dispersal kernels to incorporate a factor like annual peak flow discharge to control migration was not currently possible.

WATERHOLE PERSISTENCE

Waterhole characterisation

Using remote sensing imagery from Landsat 5, 6,7 and 8 we calculated the wetted area for each river segment in the landscape. To assess the waterhole characteristics of each river segment, remotely sensed data showing the 'wet area' was collected analysing imagery through Google Earth Engine (Gorelick et al., 2017). For each 5 km section of river, an area extending the Geofabric line 500m laterally on either side was intersected with Landsat images and cropped to a single raster image (Figure 12).

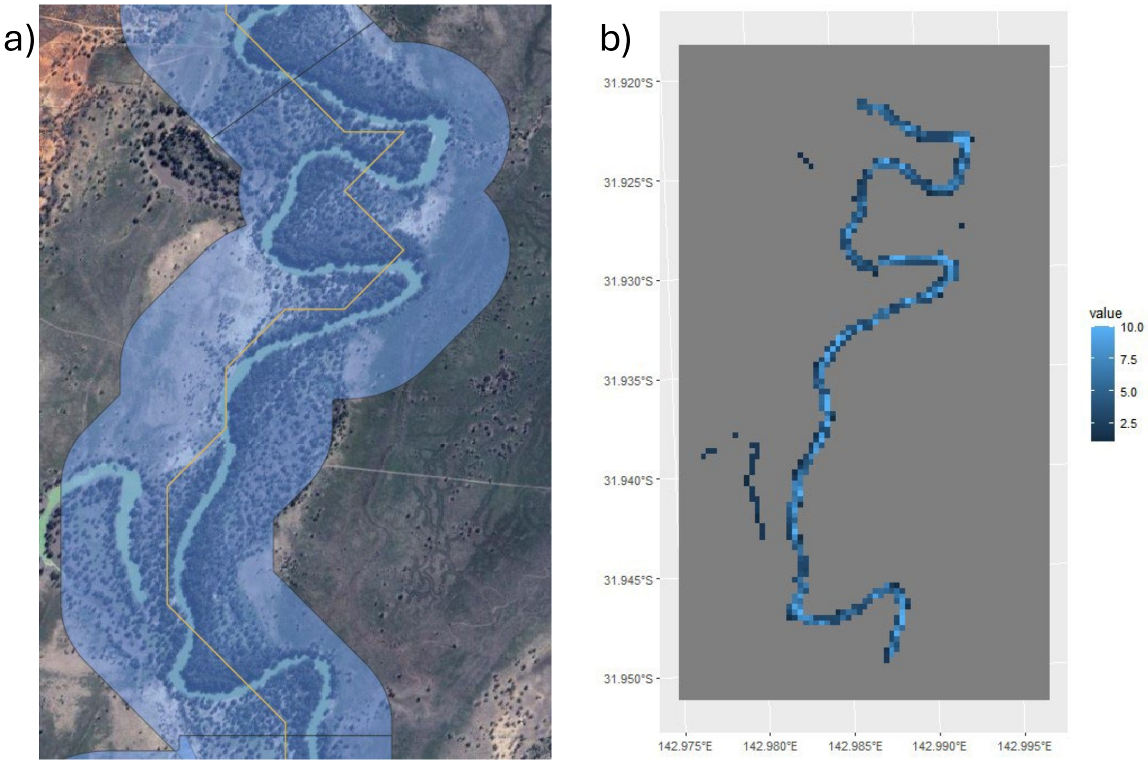

Figure 12.Representation of the processing of satellite imagery for a 5 km segment of the Darling (Baaka) River. a) Shows the pre-processed image for a single Landsat image and the 1 km by 5 km reach (shaded blue) associated with the river reach (yellow) and the b) post-processed MNDWI image using all available cease to flow images of the reach of duration into a cease to flow event (value = months of waterhole persistence)

To calculate wet area for these locations these raster images were then processed using the Modified Normalized Difference Water Index (MNDWI). This metric uses green (wavelength range 0.52 to 0.60 μm) and Short Wave Infra Red (SWIR, wavelength range 1.56 to 1.66 μm) bands to enhance open water features in remotely sensed images (Xu, 2006). The spectral calculation of this parameter is defined as:

$$MNDWI = \frac{Green - SWIR}{Green + SWIR} \tag{3}$$

Landsat scenes were aligned to 'water years', which we define as starting in the first month of the average driest 6 months across all years. Annual analysis of cease to flow conditions were built on the observed or modelled flow at the Wilcannia Gauge on the Darling (Baaka) River (Darling@Wilcannia (Main Channel); 425008). Durations of cease to flow were determined as continuous periods of flow <20 ML.day $^{-1}$ (**https://water.dpie.nsw.gov.au/__data/assets/pdf_file/0006/484863/connectivity-analysis-technical-methods-report.pdf**) without interruption greater than 10 days and binned into monthly flow categories of cease to flow spell duration.

Using this approach, we were able to model the total wet area of each of the sub-population reaches as a function of months of cease to flow duration. These areas were then used to establish the annual carrying capacity of each focal fish species given the adjusted stocking rates that we described in the "Carrying capacity and initial conditions" section prior.

HYDROLOGICAL ANALYSIS

Conditional flow probability and alternate flow conditions

To be able to calculate probable time series of cease to flow (CTF) the conditional probabilities of cease to flow given the previous year's conditions is required. To calculate conditional cease to flow probabilities for the Darling (Baaka) River we aggregated gauge data annually and characterised years based on the monthly maximum CTF duration for all months up to 6 months duration and then also CTF durations longer than six months to one year (e.g. 0:30 days, 31:60 days… 181:366 days). We initially aggregated the data to determine independent probabilities of cease to flow duration and found that cease to flow durations of up to 30 days occurred in 56.5% of years and 6.5%, 10.9%, 10.9%, 4.3, 8.7, 2.2% of years for 30 : 60 day, 60 : 90 day, 90 : 120 day, 120 : 150 day, 150 : 180 and 180 : 366 day durations respectively (Figure 11). This analysis showed that between 1972-2019 CTF periods greater than 30 days tended to have greater likelihood of occurring after years where CTF had also been greater than 30 days. Further, short duration CTF events (<30 days) have a greater likelihood of occurring after another short duration event.

Given these findings we aggregated information from the Murray Darling Basin Sustainable Yields Scenarios (MDBSY: Chiew et al. (2008)) for the Wilcannia flow gauge from datasets described in Table 4 and performed the same CTF analysis. Flows for MDBSY scenarios were also restricted to 1972-2009 to remain comparable to the observed gauge data, understanding this does miss some of the greater CTF periods in the years since. To generate likely CTF conditions for alternate scenarios and those without development on the catchment series available through MDBSY, we analysed data with the same thresholds (i.e. 20 ML.day^{-1} at Wilcannia). This was not reflective of any scenario from the MDBSY when compared to the Observed flow time series, and multiple flow limits (20, 50, 100, 150 ML.day^{-1}, Figure 12) were tested for fit.

Table 4. Murray Darling Basin Sustainable Yields Scenarios of flow for comparison

Scenario Name	Description
Darling@Wilcannia (Main Channel); Gauge 425008 ("Observed")	Observed data at Gauge
Daily_WoB_Benchmark_971	Baseline Historic data Modelled (Run- 971)
Daily_WoB_BDL_845	Historic climate with basin plan (Run - 845)
Daily_WoB_WoD_844	Without development (Run 844)
Daily_WoB_BDL_wet_894	With basin plan; second wettest result from high global warming scenario (Run 894)
Daily_WoB_BDL_med_892	With basin plan; median result from the 15 GCMs for the medium global warming scenario (Run 892)
Daily_WoB_BDL_dry_893	With basin plan; second driest result from high global warming scenario (Run 893)

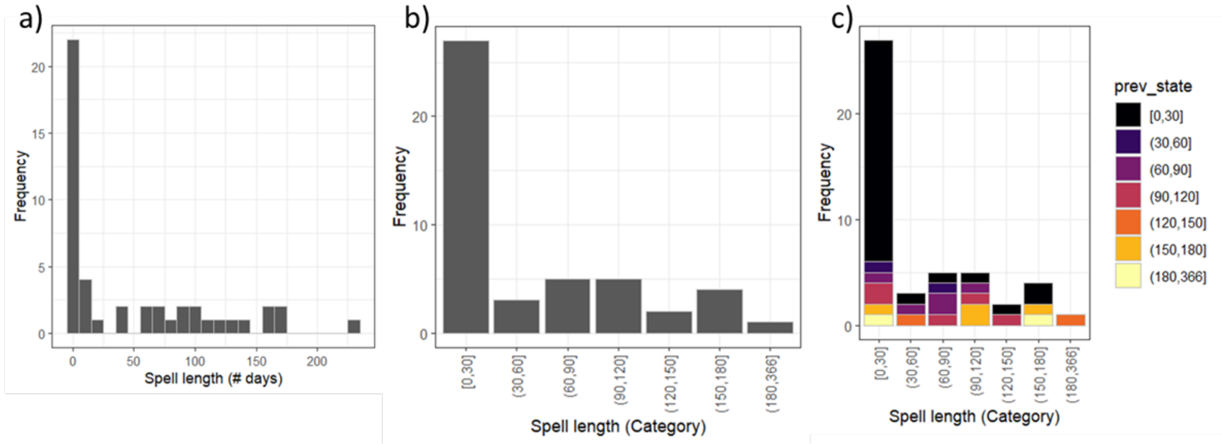

Figure 13. Frequency histograms of observed cease to flow spells showing a) the spell length b) the categorical spell distribution and c) the conditional (dependant on previous state) frequency of spell category.

Unfortunately, MDBSY was not an appropriate dataset to capture CTF events in this system and we have opted for an alternative method. Upon investigation of time series of each option (Figure 13), it can be seen that these calculated flows are a poor indicator of low and cease to flow conditions when compared to observed flows. Given these issues with the dataset we determined the use of a decision-scaling framework would be most appropriate considering the lack of modelled low flow information for the Darling (Baaka) River. This approach is commonly used when assessing risk factors with high uncertainty (e.g. future climate scenarios; Brown et al. (2012); Brown et al. (2019); Poff et al. (2016)) and given the many contributing factors to cease to flow durations (e.g. annual hydrology, water extraction future temperature change) are indeed complex we manipulated the observed cease to flow events to be of varying duration to reflect potential change as a reasonable compromise between accurate representation and complex system dynamics. Here we analysed both increased and decreased durations of cease to flow assessing a reduction of cease to flow duration of 50 10% and an increase in cease to flow duration of 10, 15, 20, 50% would provide an appropriate comparison to the current behaviour of the system and likely conditions for future climate change.

This was done by shifting the start date of a cease to flow event by the appropriate proportional duration and recalculating probabilities in the way outlined above. Given our model projects annual population estimates the maximum annual CTF spell was used as the control on our calculation of wetted area. The longest spell that could be achieved was 366 days.

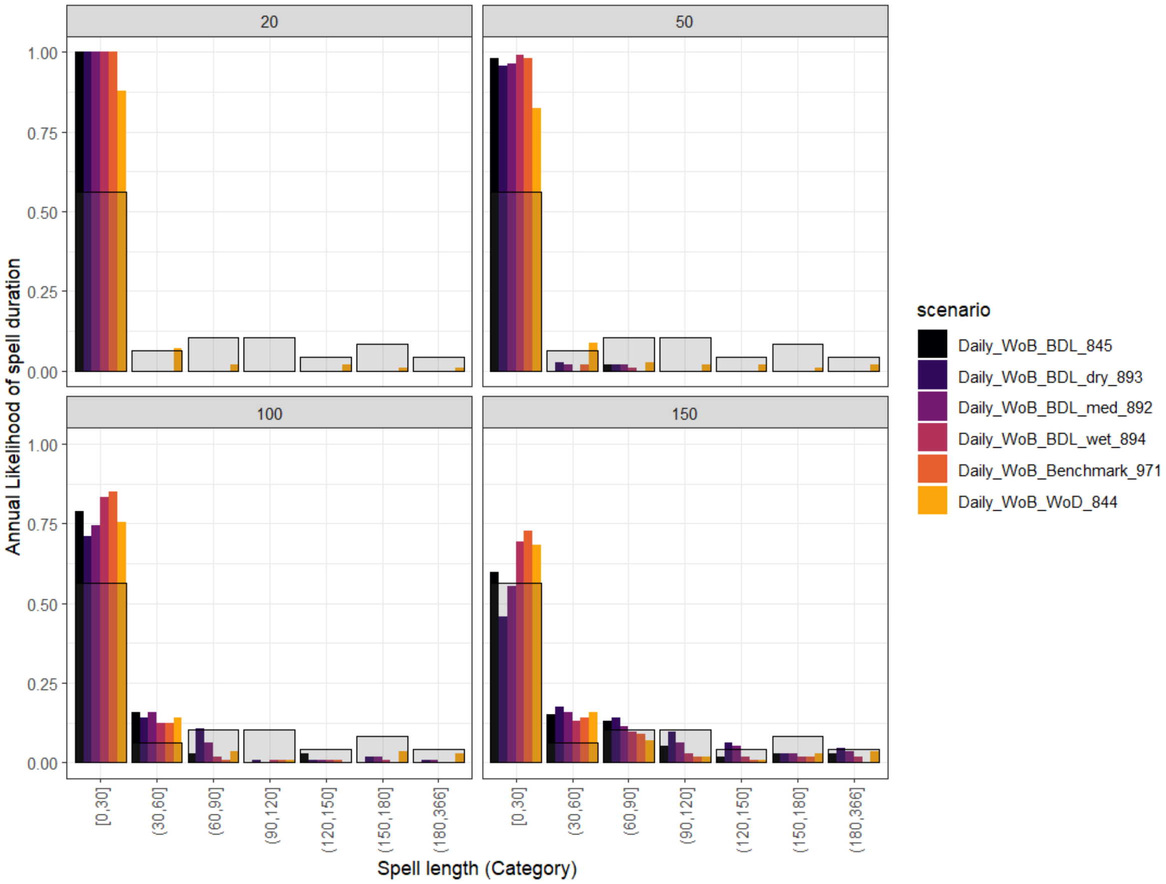

Figure 14. MDBSY cease to flow likelihoods by modelled scenario (colour) and for multiple "cease to flow" threshold volumes (panels 20, 50, 100, 150 ML day^{-1}). The translucent grey bars show the calculated independent likelihood of the observed flow time series at Wilcannia.

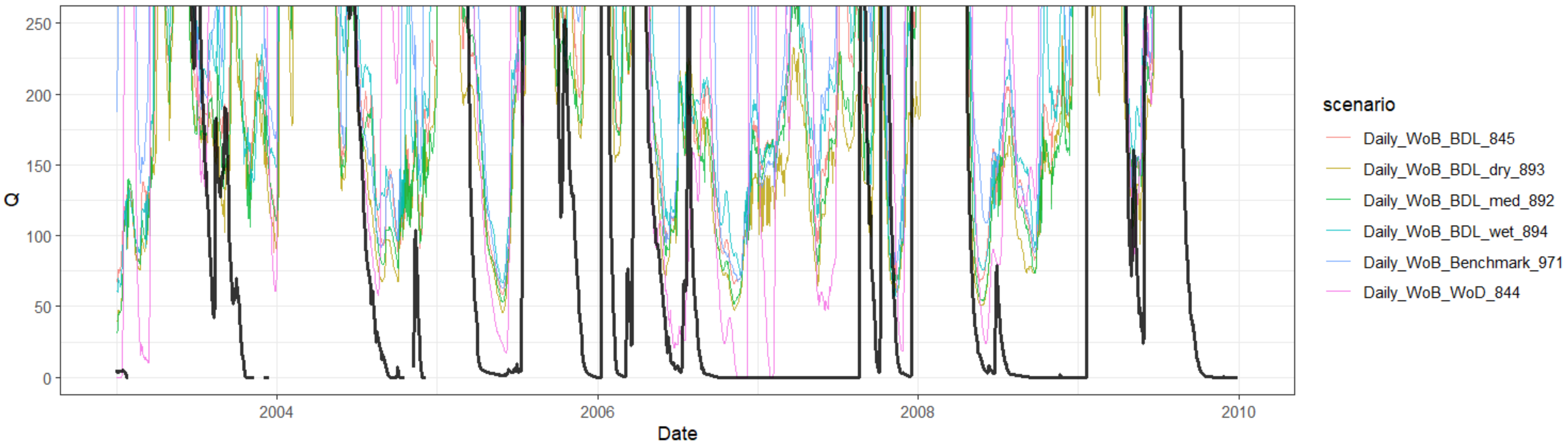

Figure 15. Time series between 2003 and 2010 of observed (black line) and modelled MDBSY scenarios.

Analysis of Lakes fill rates

The significance of the Menindee Lakes as a source population for the Darling (Baaka) River meant analysis of their volume and capacity with respect to cease to flow events was required. Understanding that the operation of these systems influences their volume mostly independently of the conditions in the Darling (Baaka) River (see Vertessy et al. (2019)) these analyses are assumed to be reflective operational practices from the reference period and do not consider alteration to the management of the Menindee Lakes. Comparison of the annual fill volumes for the four lakes being assessed showed increased frequency of CTF events was negatively correlated with cease to flow duration (Figure 14, Figure 15). This relationship was strongest for Lake Menindee and Lake Cawndilla with more variation in the relationships for the Pamamaroo Lake/Copi Hollow and Wetherell Lake/Tandure lake storages (Figure 15).

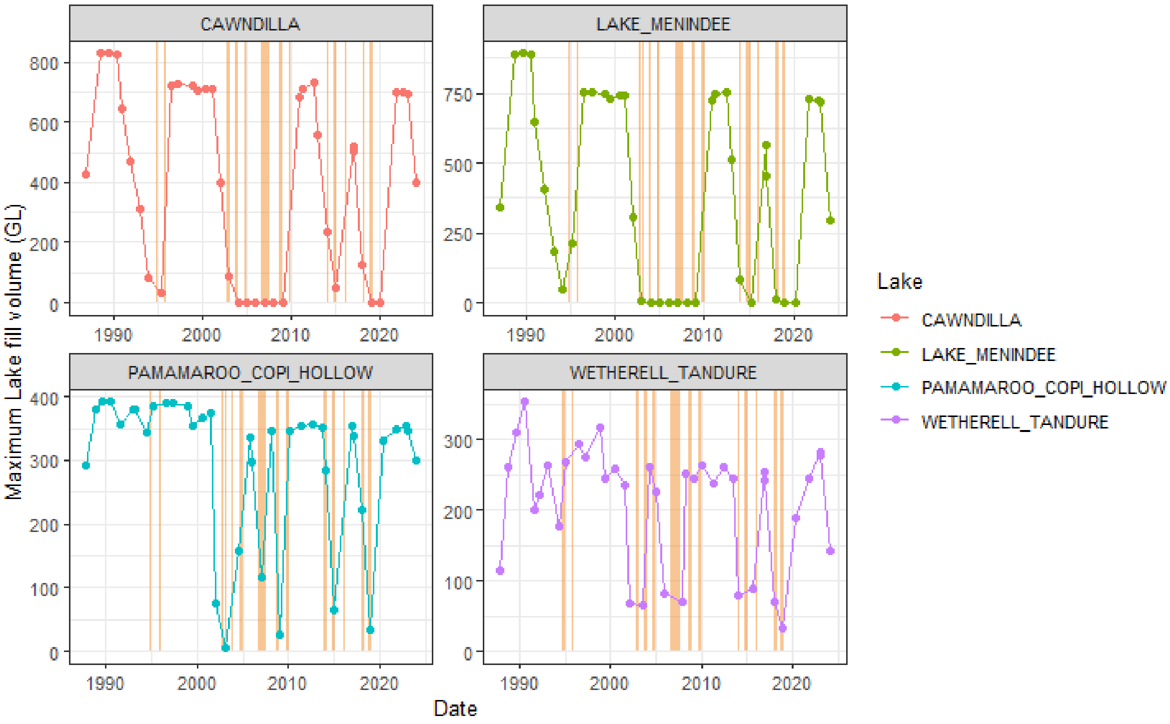

Figure 16. Maximum annual fill volumes between 1988 and 2023 for each lake and cease to flow conditions events for that year (Orange shaded areas).

While significant relationships resulted from these analyses, the range of cease to flow durations within the error of these relationships was deemed too high to be a useful predictor of volume (Figure 15). From the simulated scenarios of hydrology for cease to flow, maximum discharge of the river was also calculated. This gave us a predictor to model the wet area in each lake and required the development of relationships between maximum discharge and the storage volume of the lakes. Generalised additive models were used for this purpose considering the likely non-linear relationship between lake fill volume and wet area, with the assumption that at low volumes the relationship between wetted area and volume would be near linear though as wetted area increased the proportional changes in volume would be larger. Initial models of wet area predicted by maximum annual discharge was poor at capturing very low volumes for the lake systems and meant that regardless of the modelled conditions lakes were extremely unlikely to empty with wet areas far above 0 (Figure 16).

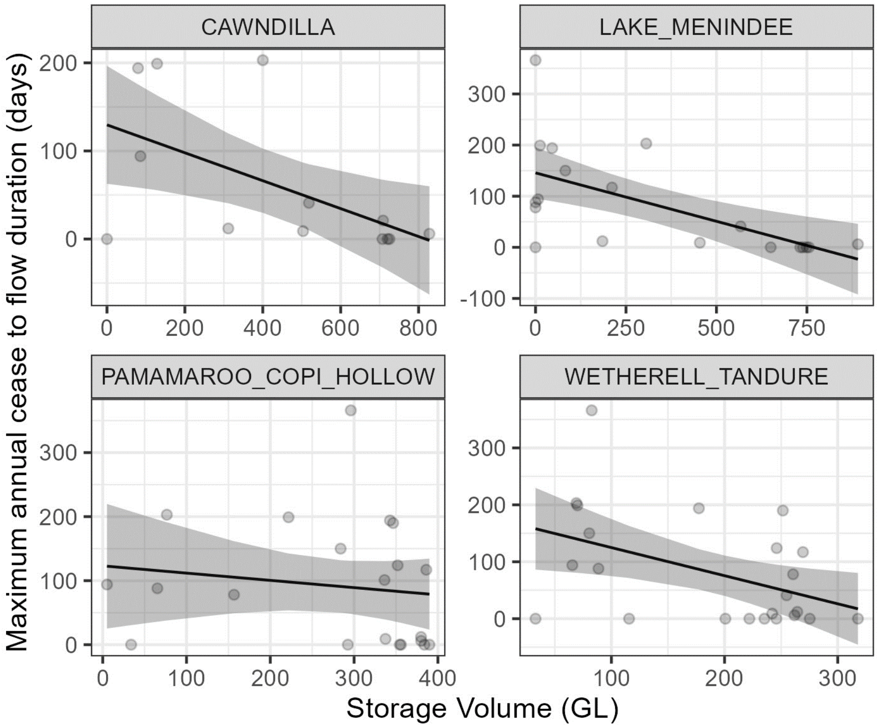

Figure 17. Modelled relationships between annual Maximum CTF duration and Maximum volume in storages.

Thus to generate a time series of wet area from maximum monthly flow we modelled storage volume as a function of maximum flow (Figure 19) and then calculated wet area as a function of storage volume (Figure 20). These relationships were less variable and reflect operational action of the system, that is, the management of storage volumes in the Menindee Lakes system is more likely influenced by hydrological conditions than cease to flow events. In this way we were indirectly able to model the wet area of the Menindee Lakes given maximum annual discharge and thus carrying capacity for the modelled species of freshwater fish.

Waterhole Turnover likelihood

Reductions in the total carrying capacity of waterholes is certainly one control on aquatic populations though the main factor attributed to catastrophic population declines in the Darling (Baaka) (Office of the NSW Chief Scientist & Engineer, 2023; Vertessy et al., 2019) is the rapid hypoxic conditions that are associated with the turnover of waterholes. While there are several mechanisms that drive hypoxic conditions in waterholes including: thermal stratification, rapid temperature change, and algal blooms, modelling this process is the focus of many other projects and out of the scope of what we could complete. Thus, in a similar fashion to the modelling of cease to flow data we have taken a decision scaling approach that incorporates variability in a factor of influence across a range of potential values. Here we have included independent likelihoods of waterhole turnover ranging across 1, 2, 5, 10 and 20 % likelihood of occurrence of waterhole turnover. If a turnover event occurred, the carrying capacity and abundance of all individuals in that sub-population became 0.

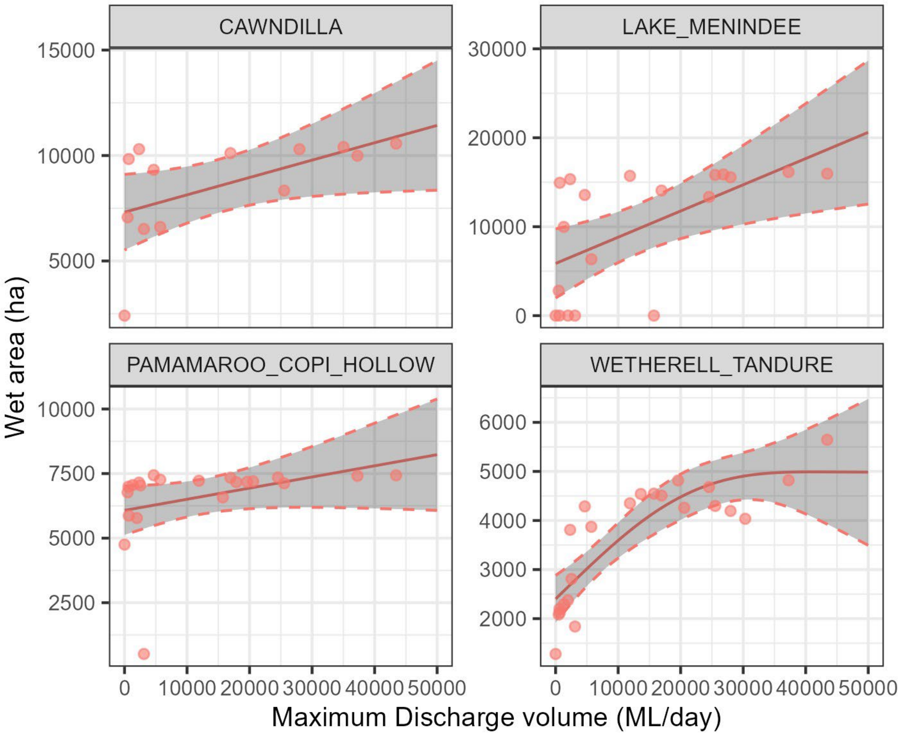

Figure 18. Generalised additive model relationships of maximum annual discharge and wet area.

Timeseries of carrying capacity

Finally, the conditional probabilities generated for cease to flow conditions and Maximum flow volume were simulated 100 times with starting conditions being drawn randomly from the distribution of non-conditional cease to flow or maximum flow probability distributions. These simulations were for a duration of 100 years and to avoid the influence of initial conditions on summary metrics for these populations, the first 10 years were removed from each simulation. For both factors of perturbation to population trajectories, i.e. cease to flow duration and waterhole turnover rate, the starting carrying capacity a time series was drawn from the probability distribution for cease to flows. This initial value was then projected using conditional probabilities calculated for each scenario of cease to flow and waterhole turnover rate. Then to incorporate the waterhole turn over characteristics for each scenario, 100 binary values were generated with the varying probabilities of waterhole turn over (i.e. turnover likelihood = 0.01, 0.02, 0.05, 0.1, 0.2). for example on average it would be expected that a simulation for a likelihood of 0.01 would have a single ‘0 event’ in 100 years where as for the likelihood of 0.2 the series on average would have 20 ‘0 events’. These binary time series were then multiplied pairwise by each year of the cease to flow carrying capacities to create a time series where

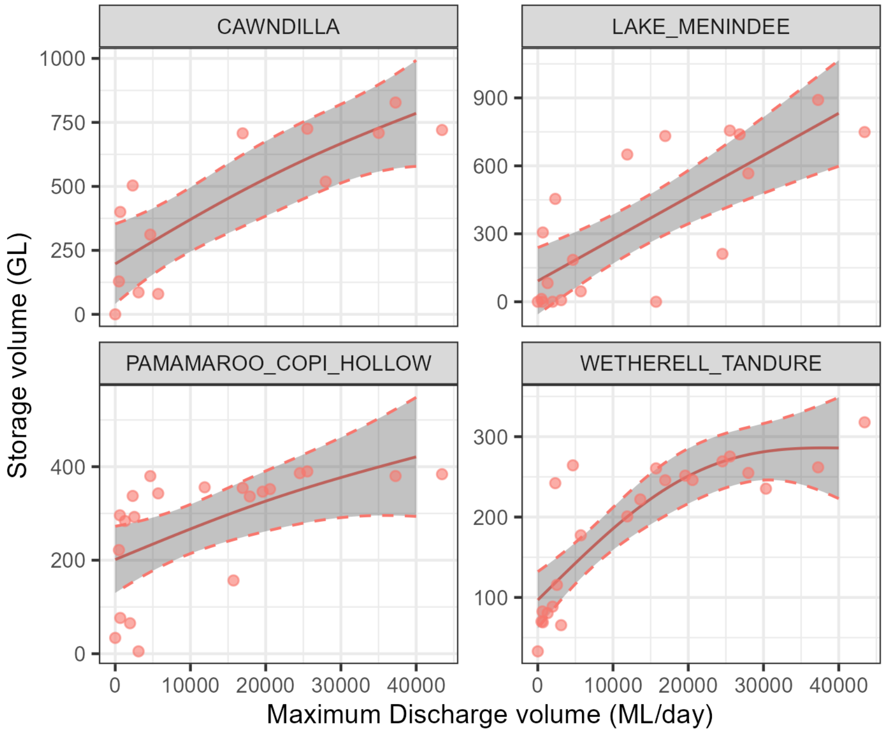

Figure 19.Generalised additive model relationships of maximum annual discharge and storage volume.

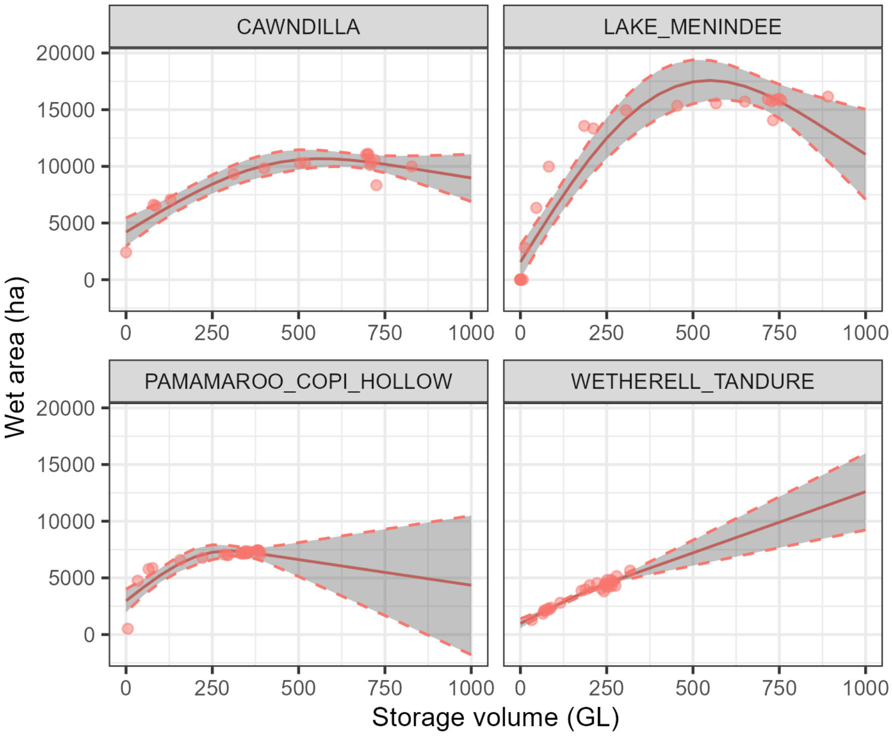

Figure 20. Generalised additive model relationships of storage volume and Wet area.

waterholes would stochastically overturn and have a hypoxic event that generated a carrying capacity of 0 for that year prior.

POPULATION MODEL RESULTS

From 100 model runs of each scenario of *cease_to_flow* and *waterhole_turnover* population abundances and quasi-extinction risk were calculated for each species to determine likely population persistence. The quasi-extinction risk was taken as the 5th percentile median abundance of the meta-population of as species across all scenarios of future change (n = 35). In addition to sub populations for the Menindee Lakes and river waterhole reaches of the Darling (Baaka) River a single node was placed at the top of the network to capture individuals moving between the northern rivers of the catchment, and a node below weir 32 to account for connectivity between the lower Darling (Baaka) or Murray and the reaches we have modelled. There locations were set with an arbitrarily large carrying capacity of 1 million which was proportionally standardised for each species (i.e. lower and upper nodes for *N. erebi,* K = 617,000).

All models point to significantly large populations of individuals in the lower reaches of the Darling (Baaka), particularly the "Segment 13", that between the Main weir and Weir 32 (Figure 22). This is a significant choke point for movement of individuals up into the catchment. There was a decreasing median abundance for all species as *cease_to_flow* conditions became longer with higher median population sizes evident in periods with shorter cease to flow durations (Figure 23). However, the greater effect on the distribution of medians for each scenario was the increasing likelihood of fish kill events from increased *waterhole_turnover* (Figure 23). Of particular note is the near complete loss of populations of *M. peelii* if waterhole turnover induced fish kills reaches an average rate of 1 every 10 years for the entire river system, plausible given recent events.

As a way of interpolating between the modelled scenarios and to provide more general understanding of how increasing dry duration and the risk of waterhole turnover interact to influence populations we used a non-linear interactive approach. Tensor product smooths between cease to flow duration scenario and likelihood of waterhole turnover, were constructed within a generalised additive model framework(Wood, 2017). This allowed the "risk surface" generally sought after in decision scaling approaches to be plotted for each species with respect to their quasi extinction (Figure 22).

All modelled species showed a decreasing time to quasi-extinction with increasing risk of waterhole turnover. Modelled results showed that median time to extinction was after or within a decade (see *M. peellii*; Figure 22) of the 100 year time series modelled for native species of the system (*M. ambigua*, *M. peelli* and *N. erebi*) when this value was below 2%. Of note here is if current conditions are not changed greatly into the future, i.e. ± 10% duration of cease to flow, we found poor outcomes for *C. carpio* in the system. This does currently account for the tolerance that carp have in the form of surface gulping air, likely a significant factor in their ability to persist through hypoxic events. However, our results also show that populations of *C. carpio* are far less likely to succumb to quasi-extinction within 100 years if cease to flow conditions are less variable than current conditions, either far shorter or longer durations.

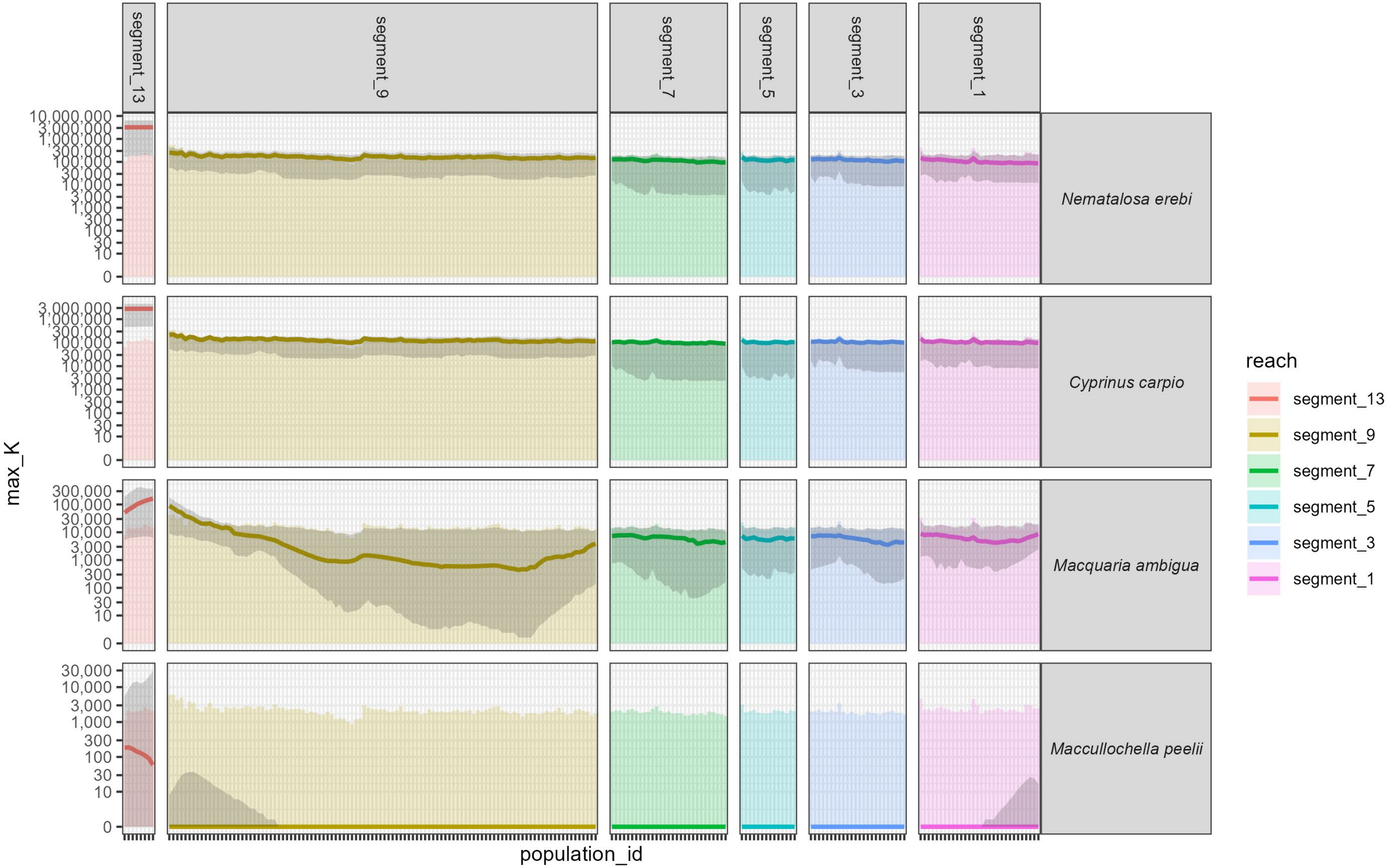

Figure 21. Median population across 100 model iterations for all scenarios. Coloured and shaded areas show the maximum carrying capacity of each sub population within a reach, lines show the median abundances across the catchment with 95% confidence in grey shading.

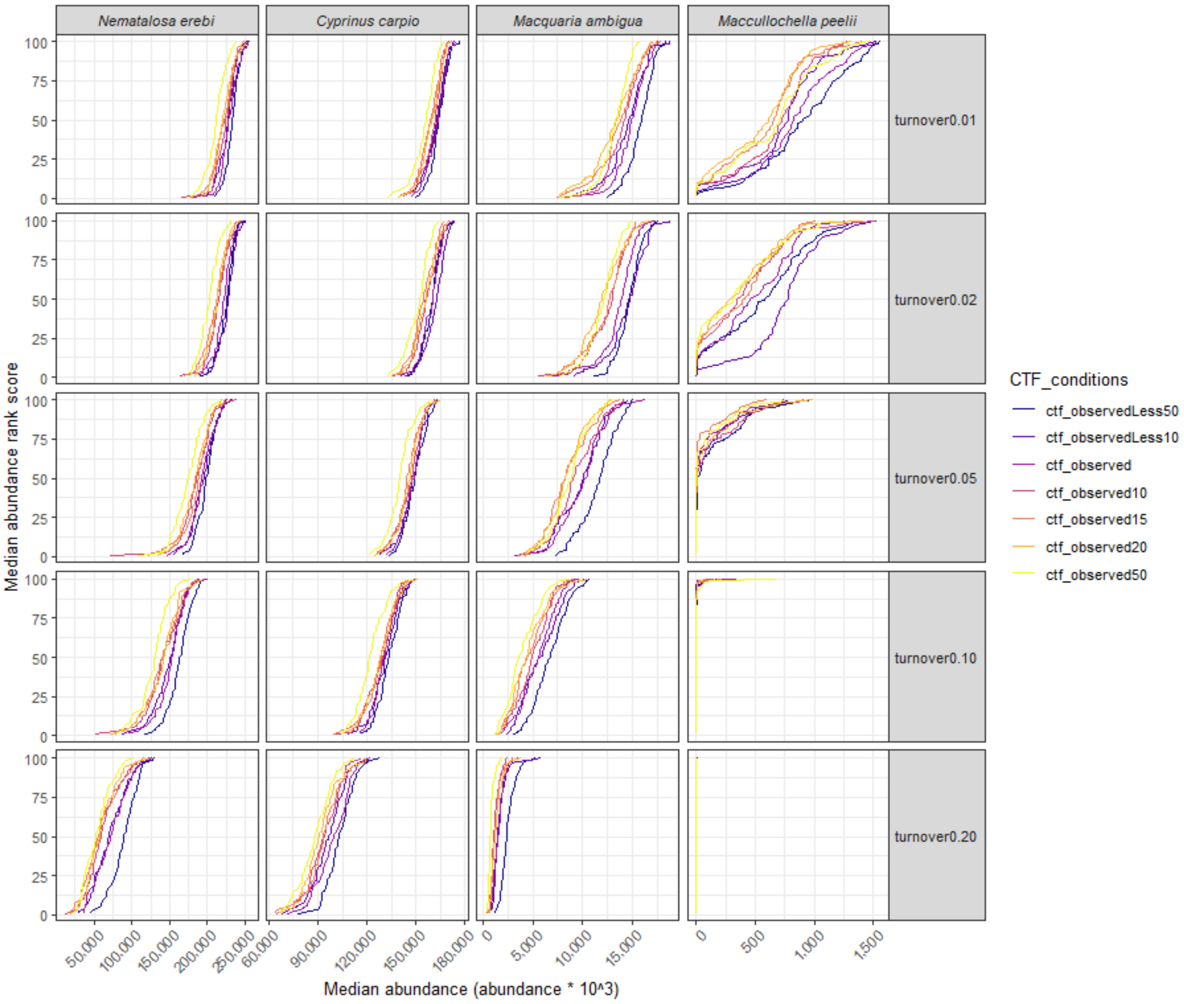

Figure 22. Median abundances of all model runs ranked from lowest median abundance to highest for each scenario of Cease to flow conditions and waterhole turnover likelihood.

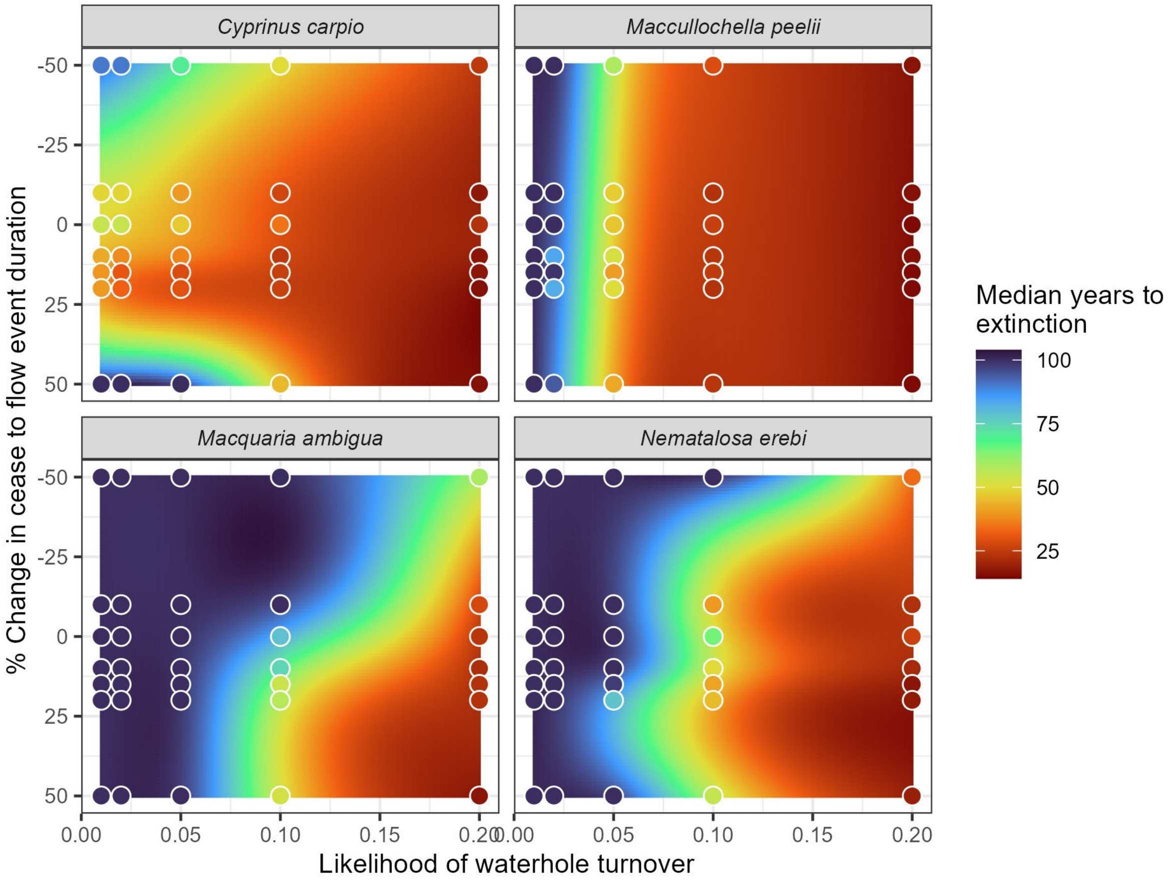

Figure 23. Time to quasi-extinction across all scenario's of waterhole turnover and cease to flow duration. Points show the median time to quasi-extinction for each of the simulated models and the surface below is the smoothed tensor spline modelled from these model results.

Discussion

The occurrence of fish kills globally is increasing (La & Cooke, 2011) and given simulated future conditions for the Darling (Baaka) system presented in this research we add quantitative projections of extinction risk and population size of several species impacted by the drivers of fish kill events. Our results corroborate the findings of contemporary reports suggesting fish populations of the Darling (Baaka) are at risk of significant local extinction and the frequency of events contributing to fish kills will increase in the system (Bice et al., 2021; Office of the NSW Chief Scientist & Engineer, 2023; Vertessy et al., 2019). Without intervention in the form of altered flow management practices and infrastructure this future is highly likely to occur within this century should current conditions remain, sooner if drying continues at the rate we have seen in the past 40 years.

Recent fish kill events (2018-19 & 2023) and generally drier conditions of the past 20 years for the Darling (Baaka), particularly for the northern basin, have left native fish populations in a vulnerable state, in dire need of intervention. *Macullochella peelii* within the reaches we have assessed, were found to have a relative fecundity of less than one, meaning populations in reaches upstream of Weir 32 are already likely unable to be self sufficient and without intervention will become extinct locally. Remnant pools that persist into cease to flow events due the influence of ground water or other sources that anecdotally support adult individuals (pers comm Jason Thiem, 2024) may have breeding potential but isolation from favourable and relatively stable environments for progeny to recruit into would cause an increasingly senescent population.

For the focal native species assessed here the most influential factor on population median abundances and subsequent persistence is increasing the frequency of waterhole turnover causing hypoxic events. Compounding this impact is the alteration of natural hydrological processes. Without barriers, waterholes would once have reconnected under flowing conditions and facilitate migrations between habitats for isolated populations. Given the largely impassable structures (until significant flows cause the drowning of these weirs) of the lower Darling (Baaka) system, particularly Weir 32 and the Main weir at Menindee isolating the “Nursery habitat" of the Menindee Lakes from areas upstream, there is limited ability for abundant remnant populations to colonise into areas effected by prolonged cease to flow events and waterhole turnover. The lower 500-km reach of the Darling (Baaka) River is a population stronghold for Murray cod and other native species, supported by lotic conditions and historic base flows (Sharpe & Stuart, 2018), this should be where we look to assist in restoring populations of the mid and upper reaches of the Darling (Baaka) thorough increased connectivity between the populations.

A lack of research using population models that represent system dynamics and conditions, which use contemporary data sources was identified as an issue and has been called for by researchers active in this research area (Fournier et al., 2021; Koehn et al., 2022; Koehn et al., 2018). Using a decision scaling approach was necessary for this work in light of available data. However, this approach highlighted that the changes to the population persistence of native fish under variable hydrological futures are sensitive to relatively small changes to turnover likelihoods. This was a far stronger population response for both median abundances and persistence across simulations than increases to modification of cease to flow durations. This highlights previous calls to action with respect to management actions that avoid waterhole stratification (Office of the NSW Chief Scientist & Engineer, 2023; Vertessy et al., 2019). Particularly in light of more variable future weather conditions contributing to stochastic events causing inversion of the water column (e.g. greater diurnal variation in temperature, increased storm events and fronts), this driver may have the greatest influence on population management of freshwater native species in this system than other measure (e.g. stocking or habitat restoration). Preventing prolonged and significant stratification of waterholes in the first case should be a priority.

Here we have built a model that is reflective of processes in the Darling (Baaka) system and reflects many of the ecological responses that have been observed in recent years, though there are some areas of future development and research. Greater understanding of the drivers of both waterhole stratification in system and likelihoods of waterhole turnover would improve these outcomes from the purely stochastic approach by correlating them to existing parts of the model including cease to flow conditions or some analogue. Additionally with respect to hypoxia there is potential that the total abundance of fish in a waterhole, not only the carrying capacity for a single species is likely to change the available dissolved oxygen and may result in hypoxic events and should be incorporated into future models. Finally, work that is currently underway to improve the ability of hydrological models to capture low flow and cease to flow events would improve the representation of conditions in a model of this type.

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