RESEARCH 4

2016-170

WILL CARP VIRUS
BIOCONTROL
BE EFFECTIVE?

NATIONAL CARP CONTROL PLAN

Development of hydrological, ecological and epidemiological modelling

This suite of documents contains those listed below.

NCCP TECHNICAL PAPERS

1. Carp biocontrol background
2. Epidemiology and release strategies
3. Carp biocontrol and water quality
4. Carp virus species specificity
5. Potential socio-economic impacts of carp biocontrol
6. NCCP implementation
7. NCCP engagement report
8. NCCP Murray and Murrumbidgee case study
9. NCCP Lachlan case study

NCCP RESEARCH (peer reviewed)

Will carp virus biocontrol be effective?

1. 2016-153: Preparing for Cyprinid herpesvirus 3: A carp biomass estimate for eastern Australia
2. 2018-120: Population dynamics and carp biomass estimates for Australia
3. 2017-148: Exploring genetic biocontrol options that could work synergistically with the carp virus
4. 2016-170: Development of hydrological, ecological and epidemiological modelling
5. 2017-135: Essential studies on Cyprinid herpesvirus 3 (CyHV-3) prior to release of the virus in Australian waters
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7. 2019-163 Understanding the genetics and genomics of carp strains and susceptibility to CyHV-3
8. 2017-094: Review of carp control via commercial exploitation

What are the carp virus biocontrol risks and how can they be managed?

9. 2017-055 and 2017-056: Water-quality risk assessment of carp biocontrol for Australian waterways
10. 2016-183: Cyprinid herpesvirus 3 and its relevance to humans
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13. 2016-152 and 2018-189: The socio-economic impact assessment and stakeholder engagement
    Appendix 1: Getting the National Carp Control Plan right: Ensuring the plan addresses
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Development of hydrological, ecological and epidemiological modelling to inform a CyHV3 release strategy for the biocontrol of carp in the Murray Darling Basin

Part A. Integrated ecological and epidemiological modelling

Peter A. Durr, Stephen Davis, Klaus Joehnk, Kerryne Graham, Jess Hopf, Arathi Arakala, Ken A. McColl, Stephen Taylor, Yun Chen, Ashmita Sengupta, Linda Merrin, Danial Stratford, Santosh Aryal, Rieks D. van Klinken, Paul Brown, Dean Gilligan

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In submitting this report, the researcher has agreed to FRDC publishing this material in its edited form.

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Executive Summary

This report details work undertaken by CSIRO and RMIT University for the National Carp Control Plan (the NCCP), between July 2017 and August 2019, and revised following peer-review in Nov-Dec 2019. It was however built-on preliminary modelling performed during 2014-16 and financed by the Invasive Animal CRC which examined the feasibility of developing a habitat suitability model for the abundance of common carp in the Lachlan River catchment and its integration into an epidemiological model that might inform a release strategy for the use of Cyprinid herpesvirus 3 (CyHV-3) as a biocontrol agent. This work concluded that developing an integrated ecological-epidemiological model was feasible but would require considerably more resources as well as a larger multi-disciplinary team. Subsequent to the formation of the NCCP, a proposal was submitted, with the following stated objectives:

1. Develop a series of inter-related hydrological, ecological and epidemiological models that will enable the development of a strategy to inform the strategic staged release of CyHV-3 so as to deliver maximum impact whilst minimizing the major anticipated adverse ecological consequence, i.e. large-scale anoxic river events.
2. Develop Big Data management and visualization systems for delivering the large amount of data that will arise from the modelling exercises in an interactive and informative manner.

Following this funding proposal being accepted, it was agreed that the adverse ecological consequence modelling was not required, as work on this was to be undertaken through a specific NCCP funded project by a team of freshwater biologists from the University of Adelaide (FRDC: 2017-055). Thus, the focus of the project became very specific, and in its initial phase the preliminary Lachlan River catchment work was finalised, with greatly expanded ecological modelling. This enabled the reconstruction of the hydrological landscape for the entire catchment from 2000 to 2016 and the assignment of a habitat suitability ranking for each river reach and waterbody. This habitat suitability model output was in turn used to develop a full spatio-temporal population projection model, which was then integrated into a CyHV-3 epidemiological model which enabled scenarios of release to be explored, with the specific aim of determining the likely reduction ("knockdown") in the carp population, given the modelling assumptions. Following on from the reporting of the results of this work, it was agreed to extend the modelling to four other catchments: the mid Murray River, the lower Murray River, the Glenelg River (in southwest Victoria) and the Moonie River (in south-east Queensland), as taken as a whole this would encompass much of the diversity of the carp habitat found in south-eastern Australia. Furthermore, the integrated modelling for these four additional catchments was extended back to 1990, to accommodate the modelling of the habitat state of the rivers and waterways before the impact of the Millennium drought (2001-2009).

Due to the complexity and scale of the entire modelling project, we have reported it in four sections, corresponding to the hydrological reconstruction modelling, the habitat suitability modelling, the carp demographic modelling and the epidemiological modelling. Some of the Sections (1 and 2 in particular) are very voluminous, and to make it more accessible, we have subsumed a lot of the technical detail of the data processing and model development into Appendices. Furthermore, as publication of this research into the peer-review literature has become a priority for the NCCP, we have formatted the reporting of the Sections as four near submission-ready drafts.

An outline schematic of the framework for the project and how this relates to the reported chapters is provided in the accompany Figure.

Although a major output of the work described in SECTION 1 was the hydrological reconstruction of the habitat and waterways for the five catchments, this reconstruction was very targeted and informed by a habitat suitability workshop undertaken during the pilot study in 2014 in which the key environmental drivers for the distribution and abundance of carp in south-eastern Australia were identified, and the manner in which they interact with each other were conceptualised into a Bayesian Belief Network (BBN). This BBN identified river flow and water temperature as the two essential parameters determining the suitability of the habitat for adult and sub-adult carp, and waterway inundation and connectivity (to enable adult carp access for spawning) for the larvae and young-of-year (YOY) stages. Several other ecological and hydrological parameters were identified as affecting habitat suitability, including aquatic productivity, dissolved oxygen and salinity. For some of these factors and for some catchments, high resolution spatio-temporal datasets were not available and, in these instances, we either used surrogate variables (e.g. temperature or habitat location for zooplankton) or left the parameter as a non-informative parent node within the BBN, in anticipation of improved datasets becoming available in the future.

Using the reconstructed hydrological datasets as input into the BBN modelling, we were able to classify each river reach or waterbody as being in a state of high, medium or low suitability for both adult/sub-adult and larvae/young-of-year (YOY) carp (SECTION 2). This classification process was repeated weekly throughout the study period, which for most of the catchments extended from 1990 to 2017. In total, this meant processing data for over 18 million BBN modelling runs, for which we needed to implement a Big Data approach, involving storing all data within a scalable PostgreSQL database, automating all process through SQL queries and Python code and running the data processing and modelling on cloud computing. A high standard of documentation was implemented, for which we used the Confluence wiki application. This application was also used to facilitate collaboration between the various teams working on the project, as well as to provide real-time feedback to the NCCP to whom we provided password protected access to the project Confluence space.

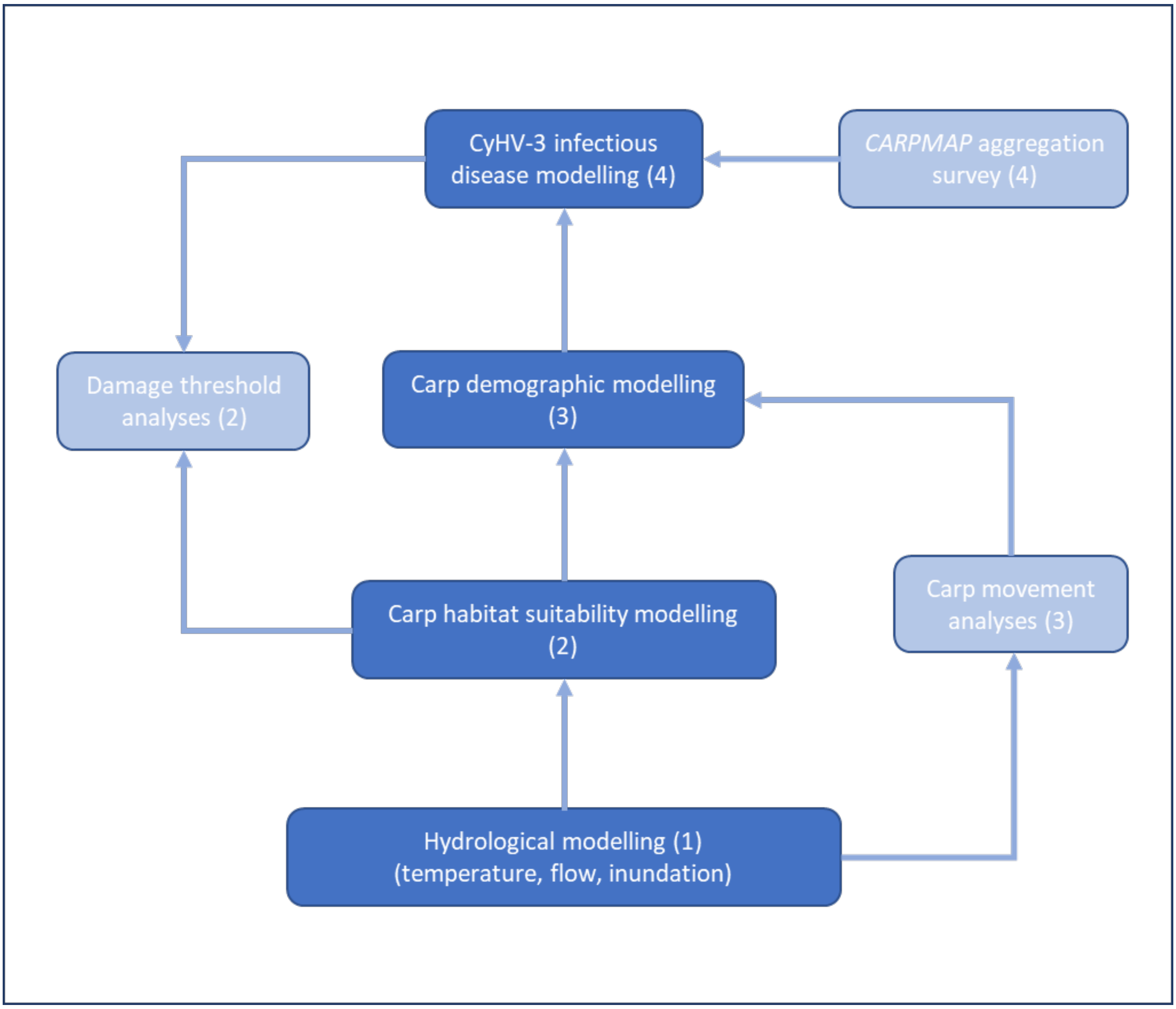
Although the output from the BBN modelling was a habitat suitability ranking, we were able to convert this into a biomass abundance density estimate (kg/ha) using conversion factors guided by expert opinion. This enabled us to estimate total biomass over presumed hydrologically distinct regions of the 5 catchments ("zones"), and directly undertake independent validation of our modelling through comparison with biomass estimates provided by the NCCP-funded Biomass project (FRDC: 2016-153), for which, after adjusting for different approaches to handling inundated areas between the two projects, showed an exceptionally high correlation ($r = 0.924$). Whilst it is then possible to derive estimates for number of carp by dividing this biomass by average weights, this is not ideal and to overcome this - and enable the implementation of population regulatory processes such as density-dependence and carrying capacity - we then used the habitat-derived biomass density as input into a full demographic projection model, the development of which is detailed in SECTION 3.

An important refinement during the development of the demographic model was a more robust definition of carp metapopulations, which in the habitat suitability modelling had been assigned as zones based on landscape features such as dams and weirs. Accordingly, we undertook a detailed analysis of the connectivity of the hydrological network and used community detection analysis tools to define 131 subpopulations in the five study catchments, thus considerably increasing the spatial resolution of the analysis. Furthermore, we undertook an analysis of an historical tagging study undertaken on the mid-Murray which was used to estimate a movement kernel which enabled us to incorporate movement into the demographic modelling.

A substantive output from the demographic modelling was the reconstruction of the demography of the carp metapopulations resolved into six age-stage classes (eggs, larvae, early YOY, late YOY, sub-adults and adults) and this enabled a baseline population size to be determined throughout the study period for each catchment, and thus a point of reference to compare the effect of a release of CyHV-3 on these populations (SECTION 4). To estimate the latter, we adapted an SEIR-type transmission model, replacing the recovered ("R") class with ones that reflect the infection dynamic of CyHV-3, i.e. a latent ("L") and a recrudescent class ("Z"). Integrating this epidemiological model with the stage transition driving the demographic model thus enabled us to fully explore effects of different epidemiological assumptions on the resultant mortality and suppression of the subpopulations following a hypothetical release. In particular, this clearly showed the importance of latency in enabling ongoing and lasting suppression of the population, which in all catchments was approximately reduced to 40% of the pre-release population. By contrast, if the model was run without assuming latency, then the population was able to recover to near pre-release levels within 5-10 years. The modelling also showed that the extent of mortality in individual carp - the case fatality rate - was an important determinant of effectiveness of the virus to suppress populations, as this suppression was successively diminished as scenarios were explored hypothetically reducing the fatality rate from 80% to 40%. This has the important implication that if genetic resistance develops rapidly then the long-term field effectiveness of the virus will be compromised, as the impact of this resistance will almost certainly be on this parameter.

Regarding the project's second objective - to develop a Big Data management and visualisation system - the first part was fully realised with the implementation of the PostgreSQL database and the use of the Confluence wiki to handle the associated metadata. Whilst good progress was made in developing an interactive visualisation system - accessible through Confluence - it became apparent during the latter stages of the project that the modelled carp population and anticipated knock-down data arising the scenarios were of more use to the NCCP, as this provided input to the operational planning required to develop a release strategy. Therefore, in place of fully realising the visualisation system, effort was expended in delivering the output from the modelling runs to the resource management team in charge of developing the detailed plan for the release.

Figure. Summary of the framework guiding the integration of the modelling, whereby arrows indicate that data and/or results were passed between the teams working on the different models. Dark blue indicates the commissioned modelling while light blue are additional analyses undertaken to support the modelling or else, as in the case of the damage threshold analyses, unifying concepts that arose during the project. Numbers refer to the Sections of this report in which the modelling or analyses is reported.



SECTION 1: Hydrological Modelling

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Abstract

Common carp (*Cyprinus carpio*) are an invasive species of the rivers and waterways of south-eastern Australia, implicated in the serious decline of many native fish species. Over the past 50 years a variety of control options have been explored, all of which to date have proved either ineffective or cost prohibitive. Most recently the use of Cyprinid herpesvirus 3 (CyHV-3), has been proposed as a biocontrol agent on account of its high specificity and mortality rates. However, the virus is known to be only effective in a permissive water temperature range of approximately 16-28°C, and to define when this will occur in the rivers and waterways of south-eastern Australia, we undertook a hydrological reconstruction of five diverse catchment areas encompassing in total a drainage area of over 130,000 km^2 over a period of 17-27 years (1990-2017). This confirmed that in the studied areas whilst the water temperatures will be permissive in the spring through to the autumn in both rivers and waterways, the time of year that this starts and ends is highly variable between and within catchments, with strong latitudinal and altitudinal gradients being evident. In the southern catchment of the Glenelg the time when the temperature enters the permissive range is 10 weeks behind that of the northern Moonie and for Lachlan River, the lowland rivers and waterway areas become permissive for virus activity an average of 7 weeks before the montane areas. Furthermore, there was extensive variation between years, being most marked for the northern Moonie River, and least for the three southern Rivers. Taken as a whole, these results show that the virus should be effective with respect to water temperature throughout the range where carp occur in south-eastern Australia, but detailed water temperature estimation will be required to determine the exact week of the start of release in any given catchment. Finally, we point out an apparent inconsistency between the length of time when the water temperature is permissive and the observations in wild carp populations in North America and Japan where outbreaks occurred predominantly in spring. This indicates the limitation of developing a “release strategy” - where, when and how to release the virus - based solely on water temperature modelling and the need to incorporate fish biology and ecology into this planning.

Keywords

Biocontrol, common carp, Cyprinid herpesvirus 3, hydrology, Murray-Darling basin, water temperature modelling

Introduction

Although common carp (*Cyprinus carpio* – hereafter referred to as carp) were introduced into south-eastern Australia in the nineteenth century, it was not until the 1970s that they became widespread and by the 1980s they were accepted as a serious invasive species (Roberts and Tilzey, 1997). This recognition followed surveys which showed that in some parts of the Murray Darling Basin (MDB) they comprised over 90% of fish biomass with associated loss of native fish species populations (Gehrke et al., 1995). Nevertheless, carp do not dominate in all hydrological ecosystems in south-eastern Australia, and the relative importance of river regulation versus the capacity of carp to be system engineers, and the processes by which they affect water quality are topics of ongoing debate (Driver et al., 1997; Fletcher et al., 1985; Robertson et al., 1997).

Whilst the role of carp as a cause or a consequence of ecosystem decline in the MDB is contentious, less so is the need to suppress their population to achieve native fish recovery (Barrett et al., 2014). Accordingly, a number of options have been explored over the past 30 years (Roberts and Tilzey, 1997) and a National Management Plan was adopted in 2000 (Carp Control Coordinating Group, 2000). Despite these, no wide-area control has been achieved, with commercial harvest, selective poisoning, genetic control and physical separation proving either to be ineffective or else cost prohibitive (Brown and Gilligan, 2014).

Based on Australia's success with the use of the myxoma virus to reduce the invasive rabbit population, Spring viremia of carp virus (SVCV) was proposed as a potential biocontrol agent for carp (Stevenson, 1978). However subsequent research found that the virus was not specific to carp (Fam. Cyprinidae) and even affected non-Cyprinid fish such as sheatfish (Siluridae), guppy (Poecilliidae) and Northern pike (Esocidae) (Crane, 1995). Subsequently, viral biocontrol was rejected as an option, and the focus of research became the potential use of sex-biasing genetic modified carp ("daughterless carp") (Thresher, 2008). Unfortunately, this technology did not fulfil its early promise, by which time viral biocontrol had become a more feasible option due to detection of Cyprinid herpesvirus 3 (CyHV-3) as a cause of mass mortality events in carp in the late 1990s (Hedrick et al., 2000). Subsequently the virus spread to numerous carp rearing countries, including Indonesia (Sunarto et al., 2005), from which an isolate was transferred to Australia's high quarantine animal health facility, the Australian Animal Health Laboratory. Subsequent research confirmed that unlike SVCV, CyHV-3 was very specific to carp, and did not infect native Australian fish (McColl et al., 2017).

A feature of many fish viral infections, including SVCV and CyHV-3 is that infection and disease only occurs naturally in a defined water temperature range (Marcos-Lopez et al., 2010). For CyHV-3 infection in carp, this has been established by infection trials to be between 16 to 28 °C (Gilad et al., 2003; Gilad et al., 2004; Yuasa et al., 2008). The existence of a "permissive range" of temperature potentially limits CyHV-3 as a biocontrol agent, particularly if rivers and waterways are only within this range for a short time period, or else the water temperature oscillates near the upper or lower threshold, such that infection might not progress to disease. Indeed, a method proposed in aquaculture to immunize carp against CyHV-3 involves infection within the permissive range, then raising it above this to prevent the appearance of disease (Ronen et al., 2003).

A simple assessment of the potential of CyHV-3 with respect to water temperature has been undertaken using a dataset from a single point beneath a weir in New South Wales, and this confirmed that the water temperature will be within the permissive range for most of the spring, summer and autumn (Becker et al., 2019). However, the generality of this conclusion across the rivers of south-eastern Australia is yet to be substantiated, and particularly whether it applies to intermittently flooded wetlands, which are important in carp's invasiveness on account of enabling massive recruitment events (Brown et al., 2005). Unlike the main river channels, there has been very little systematic water temperature data collected, on account of their often-transient nature (Humphries et al., 1999). Furthermore, because of the complex hydrology of the MDB, it is not possible to estimate simple air temperature to calculate water temperature, as has been applied in countries with more stable hydrology (Thrush and Peeler, 2012). Thus, there is a need to integrate air temperature estimates with flow estimates, whilst considering the nature of the waterbody (Webb et al., 2008).

The objective of the study was therefore to model water temperature in both, rivers and waterways, to a high degree of precision over an extended period. Due to the size of the MDB, we restricted the study to 5 catchments with a total of 132,129 km^2 drainage area that are representative for the diversity of freshwater environments, and which are also being used to model habitat suitability for carp (SECTION 2). As temperature is also identified as a parameter affecting habitat suitability, a secondary objective was to provide reconstructed hydrological landscapes, incorporating river flow, inundation, hydrological connectivity and water temperature. This in turn can be used as basis for detailed demographic and epidemiological models of carp populations and virus spread leading to a basin wide release strategy of the carp herpesvirus (SECTIONS 3 & 4).

Materials and Methods

Selection of catchments

Carp predominate in the Murray-Darling Basin (MDB) in south-east Australia, being largely absent from Tasmania, Western Australia and northern tropical Australia (Forsyth et al., 2013; Koehn, 2004). They are present, but less abundant in the coastal rivers of south-east Australia (Faragher and Lintermans, 1997). Thus, the target area for the required modelling of the temperature constraints for the release of CyHV-3 is defined to be the MDB and the coastal rivers of south-eastern Australia where carp have invaded.

Nevertheless, due to its size, which covers 1.06 million km^2, or approximately 14% of mainland Australia, it is infeasible to attempt modelling of the entire MDB at this stage. To still be able to extrapolate results to all south-east Australian rivers based on a subset of catchments we carefully selected 5 catchments representing a multitude of landforms and geo-climatic zones. Four of the 23 river valleys and their catchment areas of the MDB and one coastal catchment outside the MDB were chosen (Figure 1.1). These catchments were selected based on the availability of hydrological data and carp distribution and abundance including detailed publications on potential control options (Brown and Gilligan, 2014; Gilligan et al., 2010). The selected catchments from north to south were the Moonie River catchment in the north of the MDB, the Lachlan catchment comprising a relatively colder climate upstream region, undulating hills, irrigated farmland, weirs, dams and flat riverine plains with interconnected, ephemeral wetlands. Furthermore, we selected two substantive sections of the Murray River, in the mid and lower sections. These two sub catchments with the Murray River in the centre include extended floodplains and are vital for Australian agriculture. The fifth catchment is the Glenelg River catchment, which is a coastal river system within western Victoria. The properties of the final five study systems encompassing many of the main landscapes and habitats found throughout the wider MDB (MDBA, 2010) are summarized in Table 1.1. A more detailed description for these catchments is further provided in the Supplementary Materials S1.

A challenge in undertaking water temperature modelling for CyHV-3 is the complex hydrology of the MDB, with considerable variation in interannual flow and resultant effects on fish biology and recruitment (Humphries et al., 1999). The underlying driver for this variability is the highly cyclical rainfall pattern over much of the MDB, being driven by El Nino–Southern Oscillation (ENSO) cycles (Simpson et al., 1993). This results in periods of between 2 and 3 years where rainfall is above average, followed by periods of between 3 and 10 years where it is well below average rainfall levels (Leblanc et al., 2012). Thus, in order to inform the water temperature constraints for CyHV-3 as well as the habitat suitability for carp (SECTION 2) it was necessary to study the potential impact of variable flow over an extended time period and the connectivity pattern within the catchments. For this we chose the period from the early 1990s to 2016 for analysis comprising the period of extended drought, the “Millennium Drought” from 2001-2009 (van Dijk et al., 2013) and the following wet years with high flows in large parts of the country.

Standardised methodology for delineation of reaches

For the purpose of the current hydrological modelling, as well as the follow-on ecological, demographic and epidemiological modelling based on the hydrological outputs (SECTIONS 2-4), it was necessary to define river and stream reaches, which could be presumed to share hydrological properties, such as flow and water temperature. For the rivers and water-bodies of south-eastern Australia, there exists relatively mature geographical representations as spatial networks, which are composed of linear segments. Rivers that were of a significant size or where carp survey data existed were incorporated within the network, but minor and non-perennial streams were removed from the dataset.

The river network was extracted from a download of either the latest version of the Australian Hydrological Geospatial Fabric (BOM, 2015) for the mid-Murray, the lower Murray and the Moonie Rivers or else from VicMap Hydro (2014) for the Glenelg River. The VicMap Hydro network was preferred over the GeoFabric for the Victorian rivers on account of its higher spatial resolution (i.e. 1:25,000). For the Lachlan river network the Geodata Topo 250K Series 3 Topographic dataset was used (Geoscience Australia, 2006).

Physical, man-made structures which would be expected to act as break-points – weirs, bridges, culverts – were selected from the GeoFabric (or VicMap Hydro) and marked as reach delineators. This list of structures was cross-checked and supplemented by the list of weirs collated by the Murray-Darling Basin Weir Information System (Australian Government, 2019). In the case of NSW, a dataset on fish barrier impacts was provided by the NSW Fish Passage Program (NSW DPI, 2006). This dataset was used as the primary data source for the Lachlan and the NSW region of the Mid-Murray catchments as it contained a ranking of the impact the structure posed on fish movement across the barrier.

The spatial network was then merged to a multi-line string and a 1-km buffer was applied around these break-points to break the network at locations of impact to fish passage. The reach network was also broken at converging or diverging segments, and at river gauge locations so that observed flow data could readily be assigned. Manual editing of the reach network was then undertaken as required under specific circumstances. Each reach was assigned a unique identifier and the spatial representation was stored in a project PostgreSQL 10.6 / PostGIS 2.4.3 database for further connecting the hydrology with the temperature modelling as well as usage in a carp habitat suitability and epidemiological model for the selected catchments (SECTIONS 2-4).

For the waterbodies, we selected all entities that were intersecting a 5 km buffer of the network and where the size was greater than or equal to 2 hectares. For the Moonie and the lower Murray case studies we were able to use the spatial data derived from the Australian National Aquatic Ecosystem (ANAE) classification for the Murray Darling Basin (Brooks, 2017) and applied a filter based on an attribute for the Water Observations from Space (WOfS) summary statistic (Mueller et al., 2016). This ensured that we were analysing waterbodies that had an observed water presence of 20% over the WOfS summary period (1987-2014). In the Moonie with often disconnecting reaches we also integrated 15 waterholes (Jon Marshall, Queensland Department of Environment and Science, pers. comm. 2018). In the mid-Murray we applied different WOfS filter, as the major wetland, Barmah-Millewa Forest, has a WOfS value of 1% and the filtered result based on 20% reduced the overall number of modelled waterbodies dramatically. For the Glenelg study we used the VicMap Hydro water polygons as the spatial entity as the ANAE dataset only covers the extent of the MDB.

Summary figures of the reach delineation for the five catchments is provided in the Supplementary Materials S2.

River flow

Daily flows for all the reaches in the five selected sub-catchments were estimated for a period from 1990 until 2018 using a combination of observed gauged data and existing models. In cases where the existing observed or modelled data were not sufficient, additional methods, such as interpolation or the Rational Method-based runoff estimations were used (Titmarsh et al., 1989).

While two separate hydrological models, Integrated Quantity and Quality Model IQQM (Simons et al., 1996) and eWater-Source (eWater, 2012), are available for the Moonie River, these models only provide flows for the main river stem. To estimate flows for the tributaries and allocate flows to the reaches defined based on weirs, waterholes or other structures that might impact fish movement, we developed a simple rainfall-runoff model based on the Rational Method and bench-marked the model outputs to the observed flows at the available four gauges and modelled IQQM outputs. The runoff coefficients were estimated based on land use which is primarily grazing and dryland cropping with a small amount of irrigated agriculture.

Surface water flow estimation of the Lachlan River and its tributaries was done based on a combination of flow values derived from three sources: (i) Australian Water Resources Assessment (AWRA) output (Vaze et al., 2013); (ii) GR4J hydrologic model (Perrin et al., 2003); and (iii) NSW Government's observed data. AWRA modelled data is available for 41 stations from 1970 to mid-2014 and was used to patch missing observed data across the catchment. The GR4J model was used to determine stream flows in headwater catchments where both the AWRA and the observed data were unavailable. Given the availability of observed data at regular interval across the catchment, the confidence in overall flow estimation is high.

There are close to 200 gauges spread through the system on both the main reach and the tributaries in the Mid-Murray system, but majority of these gauges have limited data. The Murray-Darling Basin Authority (MDBA) maintains a current calibrated and validated eWater Source model (MDBA, 2019) for the system which accounts for all abstractions and environmental flow deliveries. Flow data for this study was extracted for the main reach as well as the tributaries and distributaries.

There are 10 locks in the lower Murray system which control the hydrology in the system. Daily flow volumes over Locks 1 through 6 are estimated using upstream and downstream water levels and accounts for the crest level of segments of the weir structure. Daily flow data was exported from South Australia's hydrological database. Data gaps in the flow record were patched using linear extrapolation when missing data was less than three consecutive days. In addition, a modified version of the eWater Source Murray Model (MDBA, 2019) was used to generate the modelled estimates at lock sites where data patching was required.

For estimating flows in the main reach of the Glenelg River and its 5 tributaries, we used flow data downloaded from the Bureau of Meteorology (BOM, 2019). Missing data was estimated by interpolation. In case of no gauges in a given sub-reach, data from the closest upstream gauges and any inflows from tributaries were used to estimate the flows. These flows were then cross-checked against the downstream gauges.

Further information on the hydrological regimes and flow modelling in these catchments are available in Supplemental Material S3.

Major storages

There are several large and deep reservoirs with strongly varying water levels included in the selected catchments, e.g., Wyangala and Carcoar reservoirs in the Lachlan, and Rocklands reservoir in the Glenelg. These storages were separately modelled to derive their seasonal variation in water temperature including possible stratification. Furthermore, strongly varying water levels in these reservoirs can lead to changes in carp habitat areas. For major storage entities, volumes and water level data were available to estimate surface areas. However, no water temperature data were available for these storages and needed to be modelled.

Wetland inundation

Satellite remote sensing was used to determine weekly maximum inundation areas for case study catchments. MODIS (Moderate Resolution Imaging Spectroradiometer) daily time-series images (Terra product "MOD09A"; USGS, 2010) at 500 m resolution were chosen to model inundation extent from

2000 to 2018. The MODIS inundation model was developed based on the Open Water Likelihood (OWL) index (Ticehurst et al., 2014). Taking MODIS daily images clipped to catchment boundaries as inputs, the model delivers weekly maximum inundation extent aggregated from MODIS OWL-detected daily water area within each catchment as output maps.

Landsat TM images at 25 m resolution and RiM-FIM products (Cuddy et al., 2012; Overton et al., 2010; Sims et al., 2014) at 5 m resolution were selected to map inundation areas for the time periods prior to February 2000 when MODIS data were unavailable. The advantage of the high spatial resolution of Landsat TM imagery is offset by its low temporal resolution, which can be overcome by RiM-FIM model. RiM-FIM integrates Landsat TM imagery, Lidar DEM and flow observations for estimating inundation extent at 1 GL increments in total daily flow ranging from the smallest to the largest recorded flow at a given gauge station (Sims et al., 2014). Landsat inundation mapping in this study was achieved by extracting daily inundating extent either from Landsat TM imagery directly, or from the RiM-FIM products corresponding to an observed daily flow from a selected gauge station in the catchment, and then aggregating daily extent to a weekly maximum area.

Each case study location had various datasets used. Therefore, the inundation modelling varied according to the catchment: for the Moonie, Lachlan, and Glenelg River catchments we used Landsat and MODIS OWL model, whilst for the mid and lower Murray we used the RiM-FIM model in addition to Landsat and MODIS OWL model.

More details of the inundation estimation using the MODIS OWL model and RiM-FIM are given in Supplementary Material S4.

Catchment scale water temperature modelling

Data

For the Murray River and Glenelg sufficient data is available at a large range of stations, but in the other two catchments data are sparser. For the Murray we selected only the main stations along the river or in anabranches, usually with long recordings available. For the other catchments we used all available temperature recordings with at least 2 years consecutive data with only minor gaps. However, only few stations are available with continuous recordings back to 1990 across all catchments. The water temperature station data selected for analysis is listed in Table 1.2.

Water temperature in rivers and lakes is mainly determined by the heat flux and wind stress across its surface, and heat transported by advection, i.e. flow. Daily meteorological data was sourced from SILO (Scientific Information for Land Owners), a database of historical climate records for Australia given on a 5 km by 5 km grid (Jeffrey et al., 2001). For each given location we used the nearest grid point from the SILO database. For lake temperature simulations we further used wind data retrieved from the Australian near-surface wind speed database available from CSIRO's Data Access Portal (McVicar et al., 2008). These data were compiled into gap free daily data to drive the water temperature models.

We distinguished two modelling approaches, one for rivers and shallow lakes where the vertical heat distribution is usually homogeneous, and the other for deeper reservoirs which stratify seasonally.

Lake temperature model

For lakes there exist a range of one-dimensional, vertical hydrodynamic models to simulate temperature structure over time (Stepanenko et al., 2014; Stepanenko et al., 2013). These are driven by standard meteorological data (irradiance, air temperature, relative humidity, wind speed, and cloudiness) and potentially inflow/outflow time series. Here we use the one-dimensional k-epsilon turbulence model LAKEoneD (Hutter and Jöhnk, 2004; Joehnk and Umlauf, 2001; Jöhnk et al., 2008)) to derive thermal stratification for the three big reservoirs in the Lachlan and Glenelg catchments (Wyangala, Carcoar and Rocklands reservoirs) and some shallow lakes of the system (Lake Cargelligo, Lake Brewster in the Lachlan catchment). The latter were modelled to be compared with results using the “stream” temperature model and point to potential effects of short-term stratification. For the Moonie River, the northern most catchment simulated here, the river is often disconnected during times of low or no flow, resulting in a series of waterholes (e.g., (Marshall et al., 2016)). These waterholes can, as shallow lakes do, generate a persistent stratification over short periods of time. This was tested by using the lake model on these waterholes. However, no continuous water temperature is available for these waterholes. We used data for the Brenda Waterhole in the Lower Balonne (Jon Marshall, Queensland Department of Environment and Science, pers. comm. 2018), which is in the same climatological region and thus could be used to establish a simulation model for the Moonie River waterholes. Water temperature for the Brenda waterhole was measured at a depth of about 50 cm below surface and a series of loggers further below for the period 2015-06-01 until 2015-10-07. These data were used to establish the lake temperature model. The model calibrated to the Brenda waterhole data was then used to simulate the daily course of water temperature with a depth resolution of 25 cm for 15 waterholes in the Moonie River catchment taking into account their hypsometric information and meteorological and wind data as described above.

Stream temperature model

To simulate the water temperature of streams the same principles as for lakes can be applied. Though, for large scale river systems it is advantageous to use a less complex model. Often simple correlations between air temperature and water temperature are used, however these are only applicable for a narrow temperature range. Stream temperature is dependent on the history of air temperature and flow at the location and upstream. This can be used to derive a simpler heat balance without the need to take into account the full heat balance. Here we simulate water temperature derived from air temperature and flow rates based on the model, air2stream, developed by Toffolon and Piccolroaz (2015). This model parameterises the heat balance using up to 8 parameters or a subset of these (Piccolroaz et al., 2016). To test this model tool for the five catchments we applied all possible parameterisations discussed in Piccolroaz et al. (2016) as well as simple regression with air temperature at all locations with available monitoring data (Table 1.2). Model performance was measured by calculating the root mean square error (RMSE) and the Nash-Sutcliffe model efficiency ("NSE") where an efficiency of 1 corresponds to a perfect match, 0 indicating that the model performs as well as the mean value of the observation data, and negative shows no meaningful simulation.

Results

Reach and waterbody delineation

In total 942 delineated reaches were identified within the catchments varying from 53 reaches within the Glenelg to a total of 502 in the Lachlan (Table 1.3). The number of reaches was highly correlated with the river length (r = 0.95), and thus the highest number was in the Lachlan (n = 502) and the lowest in the Glenelg (n = 53). The Lower Murray had a relatively large number of reaches (n = 179) as a result of many regulatory structures along it (n = 31). Reaches ranged in widths from a minimum width of 3m in the upper Moonie to a maximum width of 176m in the Lower Murray. Overall average widths per case study ranged from 6.8m in the Moonie, 13.38m in the Lachlan, 23.95m in the Glenelg, 46.34m and 77.38m in the Mid-Murray and Lower-Murray respectively.

With respect to the number of waterbodies per catchment, there was a strong correlation with the total waterbody area (0.85), but with several unique features for each catchment. Thus, the Mid-Murray has a relatively large number of identified water-bodies, on account of the complex hydrological structure of the Barmah-Millewa Forest, whilst the Moonie has a relatively large number of small waterholes (n = 117).

Connectivity

Numerous factors affect physical, chemical, and biological connectivity within river systems. These factors operate at multiple spatial and temporal scales and interact with each other in complex ways to determine where components of a system fall on the connectivity-isolation gradient at a given time. Here, we focus on spatial distribution patterns of wetlands. Hydrologic connectivity between wetlands and streams (or rivers) can be a function of the distance between the two water bodies. The distribution of distances between wetlands and river networks also depends on both the drainage density of the river network (the total length of stream channels per unit area) and the density of wetlands. In general, wetlands closer to the stream network will have greater hydrologic and biological connectivity to downstream waters than wetlands located farther from the same network. However, due to variability in factors such as topography, slope, and soil permeability, so more distant wetlands can have higher connectivity than wetlands that are closer to downstream waters. Reach connectivity varied significantly between wet and dry years (Table 1.4). Especially for those catchments with perennial streams and waterholes, where the Lachlan has a 6% connectivity between reaches in dry years but 66% in wet years, similar for the Moonie with 8.8% versus 32.8% in dry and wet years, respectively. For the Mid Murray connectivity is nearly always given between reaches while reach to waterbody connectivity is smaller. The Lower Murray is well connected between reaches even in dry years and also the reach to waterbody connection is relatively high with 79.7% in wet and 38.5% in dry years.

For carp movement as well as virus spread the connectivity of wetlands laterally connected to the main river channels plays a dominant role. Due to their shallowness and thus usually homogeneously mixed situation and low to no flow conditions their temperature can be modelled by the river water temperature model using no-flow input, a special case of the general river water temperature model.

Flow

Estimated flows in the five systems matched closely the observed flows where available, with coefficient of determination (R^2) values between 0.8-0.99. Figure 1.2 shows a comparison between the predicted and observed flows in the Mid-Murray system. For the Moonie flows tend to be lower with higher seasonality compared to the Mid and Lower Murray system.

For water temperature modelling the low flows or even vanishing flows in the northern catchment and to some extend in the Mid Murray flow is not a large contributor to temperature variation. This can be different during large flows in the Lower Murray or the Glenelg, where heat transport through flow might impact water temperature.

Water temperature

Lake model

Lake thermal stratification simulated with LAKEoneD shows strong stratification for the deep dams. For Lake Wyangala (Lachlan catchment) this leads to a permanent low bottom temperature over the year with a small window of whole-lake mixing during winter (Figure 1.3a). Overlain in Figure 1.3a is also the mean daily air temperature which on its own is not a good predictor for the surface temperature. Comparing results of simulations with the more complex lake model and the stream model driven by only air temperature for shallow Lake Brewster (Lachlan catchment) shows that surface water temperatures are equally well simulated (Figure 1.3b). We therefore used the stream model with no-flow input as standard water temperature simulation for all shallow water bodies.

As the deep reservoirs simulated in this study have a relatively cold hypolimnion, the water temperature at the dam outlet can be low, depending on outlet depth and water level. This often leads to downstream cold water pollution (Lugg and Copeland, 2014)). This effect can be seen in the water temperatures downstream of the two large dams in the Lachlan catchment which are significantly lower than stream temperatures in neighbouring reaches. A more detailed river model including dam operation would be needed to model this type of cold water pollution (Sherman et al., 2007). As the stream model simulates the water temperature based on "learning" from historic data it will generally generate adequate water temperatures, as long as dam operation is similar in simulated years. The current model cannot cope with changed dam operation under strongly fluctuating water levels, or climate change in future conditions effecting downstream stream temperatures in a different way. However, this effect is limited to a small number of upstream dams only and will not significantly alter habitat and virus spread based on water temperatures as simulated for the five catchments. In river reaches potentially affected by cold water pollution the virus release strategy must be analysed case by case in close relation with dam operation.

Stream model

Stream water temperature is available at many gauges in the five catchments, recordings usually starting around year 2000. Only a few stations have longer time series available. Models with 3, 4, 5, 7, and 8 parameters in air2stream as well as a regression with air temperature were tested. The simulated water temperature is exemplified for the Lachlan River at Corowa (station 412002). Figure 1.4 shows the entire simulated period, the annual cycle over a period of 4 years, and a detailed view of the seasonal cycle for the 2010/11 year. air temperature is overlain on the plots for water temperature and flow rates is shown in a separate plot. The best models are achieved using parameterizations 7 and 8, which include stream flow as predictor (Table 1.3). Models not including stream flow generally are less optimal. However, in cases where there are no flow models 8 and 4 generate non-valid temperatures due to a divide by zero operation. We therefore generally used model 7 depending on the NSE value, as no-flow conditions are common in the region. The simple regression model with air temperature in all cases resulted in inferior simulations and should be avoided when predicting water temperatures.

For the specific case of the Moonie River, separating in a series of disconnected waterholes during no-flow conditions, we simulated 15 waterholes using the lake model and compared with the stream model using only air temperature as predictor variable. The different waterholes are in the same climate region and thus their water temperature is similar, only showing variations based on their different hypsometry (see Supplementary Material S5 for hypsometric data and simulation details). The lake model was calibrated using a small set of continuous data available for the Brenda waterhole in a neighbouring catchment. Figure 1.5 shows simulation results for surface water for waterhole at Fenton, compared to recorded water temperatures nearby at station 4170204A (Moonie at Fenton). The simulations of the two different models show again good performance with regards to the observations. Thus, also for this partially disconnecting river system the air2stream water temperature model shows good simulation performance. In general, the NSE for the simulations using air2stream with the 7-parameter model is in the range above 0.85 for all stations in the five catchments.

The stream model represented measured water temperature very well in all 64 locations with available temperature data in the five catchments. Based on the reaches defined for the catchments we then selected the closest grid point from the SILO climate database and used mean air temperature for this point to simulate the water temperature in this reach using the closest available water temperature model. For the three large reservoirs in the Lachlan and Glenelg catchment we used the lake model to derive surface water temperature.

Modelled water temperatures are available for a time period from 1990 to 2018 for all 942 reaches to be used in further analysis and as basis for ecological and epidemiological models together with flow rates and inundation data (see SECTION 2-4).

Further background on water temperature modelling results is presented in the Supplementary Material S5.

Water temperature and permissive virus activity

Virus activity is dependant on water temperature. Assuming a permissibility range of 16 - 28 °C we can show the changes in timing for positive activity in all five simulated catchments. Figure 1.6 represents the monthly statistics (box plot) for selected reaches in all 5 catchments ordered from north to south superimposed with the band of assumed range of virus permissibility. Windows of opportunities for a virus release are strongly dependent on geoclimatic location. While in the Moonie and the lower regions of the Lachlan the summer months are potentially too warm with respect to permissive water temperature, the lower Murray and Glenelg River sections show that summer water temperatures are in the optimal range. This also means that the window of opportunity is smaller and broken up in a pre and post summer period in the northern catchments, while for the more southern rivers a single window of opportunity reaching from Oct./Nov. until Mar./Apr. is possible. In the case of stream reaches experiencing cold water release from upstream dams (see the Lachlan example in Figure 1.6c) the whole year is not or only sub-optimal with respect to virus activity. This implies that dam releases must be done in accordance with a release strategy.

However, this summary picture of the average seasonal cycle does not show the strong interannual variability, nor does it differentiate the distribution of permissible rages and non-permissible ranges over years or show clearly the north-south gradient in permissibility range in its full. For this we can concentrate on the number of reaches in each catchment where the temperature for virus activity is permissible (here 16-28 °C). Figure 1.7 shows the seasonal variation by plotting all simulated years for each catchment. In the Moonie the range can be met over most of the year with a small non-permissible period during winter when temperatures become too cold on average. However, the interannual variability is high in the rest of the year. While the Moonie shows a very high interannual variability in reaches in the permissible range, the other four catchments show clearer periods of permissible ranges being largest in the Lower Murray and Lachlan. While Mid Murray and Glenelg show smaller periods. This can be attributed to more pronounced winter-summer temperature regimes. A detailed analysis of the first and last week where temperature is in the permissible range is given in Table 1.6. On the rising limb of temperature during spring the permissive range is reached (median value) in week 39 for the Lower Murray and week 46 in the Moonie. Beside this general difference between catchments there is also an altitudinal difference. In the southern catchment of the Glenelg the time when the temperature enters the permissive range is 10 weeks behind that of the northern Moonie and for Lachlan River, the lowland rivers and waterway areas become permissive for virus activity an average of 7 weeks before the montane areas. Based on Figures 1.6 and 1.7 one could set up a general rule for virus release taking into account interannual climate variability and thus changes in water temperature. To support this further, one can plot the annual cycle of reaches which are below, above or within the permissible range, and adding the information when reaches are likely not connected, i.e. periods with no flow (Figure 1.8). This shows clearly, that in the Moonie disconnection, and thus waterholes are a common phenomenon, in which case a virus release is not recommended as fish to fish contact as the main mechanism of virus translation is not effective, even when water temperature would allow this. This can happen in reaches in the Lachlan, Mid Murray and Glenelg as well, but is unlikely for the Lower Murray. The latter shows a regular seasonal cycle of permissible range for virus activity with less interannual variation. Water temperatures inhibiting virus activities are not very common in all five catchments during times of free-flowing water.

For a virus release it is not only necessary that the momentary water temperature is in the permissible range but that the permissible range is sustained over a longer period to allow virus transmission. The consecutive number of weeks water temperature is in the permissible range is shown in Figure 1.9 as box plot for each catchment. It shows clearly, that the permissible range is reached on average in only 5 weeks in the reaches of the Moonie. It is around 12 weeks in the Lachlan, Glenelg and the Mid Murray, although all three catchments have significant different temperature ranges. This shows that water temperature alone is not sufficient to determine the permissible periods for virus release. Here connectivity plays also an important role. In the well-connected Lower Murray the water temperature will be the main factor for defining a permissible range of virus activity seen in a large range of 13 to 29 consecutive weeks, significantly larger than in the other four catchments.

Discussion

Defining constraints for carp herpesvirus release in a large connected river basin needs the interplay of all kind of modelling and computational techniques to be successful. Large scale hydrological models are available for parts of the Australian system, or world-wide. The status of connectivity between water bodies over large regions can only be achieved by using remote sensing technology. Connectivity might be a lesser issue in regions with regular flow characteristics but is an essential part of flood inundation modelling and like here virus spread modelling in slow flowing, lowland river systems. The high variability of climate conditions in Australia driving large variability in flow over seasons and interannually in Australian river systems made it necessary to include a dedicated component of flow and connectivity modelling for our task. Going a step further, we included a region wide model for water temperature simulation based on basic meteorological data readily available for the whole south-east Australian region, a size of France and Germany together or one third of the entire Mississippi basin. This unique combination of large-scale modelling is able to provide essential input to facilitate further modelling of carp habitats (SECTION 2), population dynamics (SECTION 3), and finally the epidemiological modelling to predict how CyHV-3 might spread across the hydrological landscape and result in population suppression (SECTION 4).

Our reconstruction of the hydrological environment over such an extensive area and time period at a fine spatiotemporal scale was only made possible by explicitly adopting a Big Data approach. The definition of what exactly defines “Big Data" is contentious, but the consensus is that it constitutes IT systems for rapidly processing and integrating large volumes of data which are informative to end-users for decision making. These criteria are generally summarised as the three “v” terms of Big Data: volume (amount of data), velocity (speed of data processing) and variety (different data types) (Gandomi and Haider, 2015). Since this conceptualisation, other “v” terms have been added: veracity (indicating that error trapping processes can remove erroneous data), validity (such that the processes are replicable and follow quality standards of data management and processing) and value (emphasising that the Big Data system needs to be useful). Applying these concepts to our reconstruction of the river and waterway environments, it was necessary to handle a moderately large volume (at approximately 1.8 TB) of very diverse data types and formats, the latter ranging from raster satellite imagery to stream segments to time-series of flows. Due to the anticipated importance of the results from the modelling (i.e. the value), much effort was needed to make the science transparent and replicable (i.e. valid and veracious). To achieve this processing was coded and input/output for all steps stored within a scalable PostgreSQL database with regular backup and retrieval systems. The only Big Data requirement not particularly important was processing speed, although in practice a cloud computing infrastructure was used for all runs.

In practice the greatest challenge faced for the river and waterway environment reconstruction was the availability and quality of the input data. This applied particularly with the hydrology for the rivers and streams away from the main channels (for which there is in general little flow gauge data) and especially for the non-River Murray catchments. Thus, for example, whilst it was possible to obtain quality flow data for the main channel of the Lachlan River catchments for the entire study period, for the tributary rivers and streams this required that rainfall-runoff modelling be undertaken, and quality data arising from this was only available from 2000 onward.

Similarly, to estimate the timing and area of inundation of wetlands and floodplains, for the Murray River we could use output from the existing RIM-FIM inundation model, for the other catchments - for which this modelling has not been applied - we needed to rely on satellite imagery for which there were a number of inconsistencies when the imagery from Landsat TM and MODIS were compared, due in part to their different spatio-temporal resolution, i.e. Landsat's 16 day frequency cannot pick up highly ephemeral water-bodies whilst MODIS with a spatial resolution of 500m resolution cannot detect small permanent ones (Chen et al., 2014). An additional problem of using satellite imagery for estimating inundation is in detecting water presence in highly vegetated areas such as the Great Cumbung Swamp in the Lachlan River, as the overlapping of vegetation and water within a pixel mis-classifies the pixel to vegetation and not swamp or highly vegetated wetlands (Mueller et al. 2016). It is therefore probable that we underestimated the extent of inundation in this area, as compared to the Barmah-Millewa Forest in the mid-Murray, where the inundated areas were estimated by the more precise RiM-FIM modelling. Even then, the RiM-FIM model can only estimate the area based on the flows of the associated river gauge, and in some areas, such as Lake Victoria on the lower Murray River or Lake Moira within the Barmah Forest when flows are below the commencement to fill value and yet there is standing water, the predicted water area may not be accurate.

Water temperature is an essential parameter in developing models of the potential behaviour of CyHV-3 in natural populations of common carp. Not only can it have a direct effect on virus replication within infected fish - with the permissive range generally considered to be between 16 and 28 °C - but water temperature has strong effects on reproduction and therefore spawning aggregation and recruitment of susceptible juveniles into the population. Furthermore, water temperature is an important factor in the habitat suitability of rivers and wetlands for carp, and thus their population density. Here we established a general method for a landscape level reconstruction of the hydrological environment (1990-2017) across five catchments in southeast Australia to define water temperature constraints for the release of the biocontrol agent, Cyprinid herpesvirus 3 (CyHV-3) to control common carp (*Cyprinus carpio*). The water temperature simulated here for the five catchments can be used to set up a physical based release strategy considering the diversity in water temperature on a north-south gradient and within the catchments over a seasonal cycle as well as flow and connectivity between water bodies. As water temperature readings from gauges in this large system is sparse and hardly available for periods before 2000 we used the available temperature data to set up water temperature models driven by air temperature and flow (Piccolroaz et al., 2016) for specific locations and generalizing them for the entire catchments and for the whole time period. This approach is easily scalable to the entire south-east Australian region or even continental wide.

For deep lakes water temperature is not varying laterally but with depth, leading to a different type of habitat separation. Stratification will be persistently present in deep lakes and shallow lakes or river reaches might show non-persistent stratification during warm spells. This behaviour was simulated using a hydrodynamic model accounting for the full heat balance, needing additional computational resources and a more detailed database on local meteorological data as well as continuous water temperature recordings at multiple depths, which in general is not available for most deep lakes or reservoirs in Australia. Furthermore, the release of cold bottom water from reservoirs can lead to downstream cold water pollution, which must be considered for virus release strategy.

In general, water temperatures of Australian rivers and waterways are within the permissive range for CyHV-3 activity for periods in spring, summer and autumn, which is in agreement with postulates from Becker et al. (2019). However, those periods are varying in extent and occasion depending on their geoclimatic position (north-south, altitude). The time of year that this starts and ends is highly variable between and within catchments, with a strong latitudinal and altitudinal gradients being evident The interannual variability can be large and any release strategy must determine the right timing between different regions to be most effective. Becker et al. (2019) only looked at upstream river reaches down to the Mid Murray set in a very confined region of the basin and even affected by cold water pollution to some extent which is common but not a general feature for the waterways in south-east Australia. They could conclude that for those, very limited, examples the permissible range of virus activity was met for large periods of the year. Here we have shown, that the picture is much more complex and must differentiate between catchments in different climate zones, downstream of dams, depending on connectivity between water bodies. A simple look at water temperature in a single region would bias the conclusions of viability and effect of a virus release. By contrast, though examining water temperatures across catchments in different climatic regions in south-east Australia we provide an overview of possible periods of opportunity for virus release depending on water temperature as well as flow and connectivity. This Big-data approach yields a much more varied picture and shows that a virus release strategy must be accompanied with detailed hydrologic and climate studies in the catchments to cope with the large variability of climate, water temperature and flow characteristics throughout south-eastern Australia.

Whilst we show that the water temperature is generally permissive for virus activity during extended periods in the spring, summer and autumn in the rivers and waterways of south-eastern Australia, nevertheless, it is premature to conclude that the virus will actually result in carp mortalities. Thresher et al. (2018) collected data on fish kills from North America associated with CyHV-3 and showed their occurrence in natural populations only during the spring. The same was evident in Japanese records of CyHV-3 outbreaks, where although autumn outbreaks occurred, these were mainly in aquaculture farming

(Sano et al., 2004). The predominance of outbreaks in spring in wild carp populations in Japan has been hypothesised to result from the direct contact which occurs during the spring spawning period (Uchii et al., 2011). This suggests that in order to predict the impact of CyHV-3 on carp populations in south-eastern Australia, there is a need for a fuller understanding of the demographic structure of carp over seasons (SECTION 3) and the clarification of habitat structure in the basin to determine hotspots of fish aggregation during spawning (SECTION 2).

Conclusion

Using different model tools for streams and lakes we were able to set up a unique, first of its type model to describe waterbody connectivity, flow and water temperatures across five catchments the size of Greece (>130,000 km^2). The choice of models was guided by easy application in data sparse regions, driven by readily available gridded meteorological data, gauged and modelled flow data and remote sensing imagery. It was not the aim to model individual river reaches, wetlands or lakes including all local characteristics, e.g., along a shaded reach or cold water pollution downstream of large dams. The model system was integrated in a database system embedding this big data approach capable for generalizing it across the entire south-east Australian region, a size of one third the entire Mississippi basin, or one fifth the entire Amazon basin.

The results of the hydrological reconstruction across five very distinct regions in south east Australia has highlighted the large variability in connectivity, flow and water temperature in both space and in time. This variability leads us to conclude that a small-scale approach cannot be used to give a general answer to timing, location and staging of a CyHV-3 release across the wider region. Furthermore, the Northern Hemisphere experience of outbreaks occurring in wild populations predominantly in the spring suggests that the water temperature modelling alone cannot be used as a basis for developing a strategy for the optimum release of the virus. Thus, to achieve this goal there is a need for integrated modelling of the biotic factors affecting carp populations, such as movement, reproduction and recruitment, and how these might interact with the epidemiology of the disease induced by the virus. We conclude that whilst temperature modelling is certainly essential for developing a release strategy for CyHV-3, it is not by itself sufficient, and further integrated modelling is required (SECTIONS 2-4).

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Tables

Table 1.1

Summary statistics of the key hydrological properties of the five studied catchments.

	Glenelg	Lachlan	Lower-Murray	Mid-Murray	Moonie
Reach (No.)	53	502	179	75	133
Water-body (No.)	860	1,113	1,426	2,645	140
Hydrological Zones (No.)	4	5	10	11	7
Modelled Drainage area (km^2)	12,973	86,554	4,933	11,995	15,674
Modelled River Length (km)	1,056	5,218	871	1,051	1,325
Modelled Water body area (km^2)	345	1,011	394	1,339	21
Downstream flow (ML/day)*	21.58 (0; 835.78)	41.18 (0; 1,273.57)	3789.29 (37.50; 41,491.59)	762.14 (0; 12,938.49)	0.04 (0; 348.56)
Median (range) Temperatures (°C)	14.86 (6.81;27.30)	18.12 (4.80;35.78)	18.62 (9.81; 29.66)	17.44 (7.60; 29.50)	20.45 (8.32; 30.54)
Connectivity (% connected) Rivers	74.58 (49.4; 89.03)	77.85 (66.44; 87.83)	98.75 (97.88; 99.32)	88.36 (75.65; 96.70)	20.18 (9.52; 35.21)
Connectivity (% connected) Waterbody	0.35 (0.35;0.35)	1.36 (0.64; 6.35)	50.13 (24.57; 75.15)	17.86 (12.22; 28.77)	15.96 (5.01; 26.22)

Table 1.2

Water temperature data used for temperature simulations in the 5 catchments.

Catchment	# stations	Total time span [years]	Average time span [years/station]
Glenelg	10	160	16
Lachlan	24	271	11
Lower Murray	15	242	16
Mid Murray	14	287	20
Moonie	1	6	6
Total	64	966	15

Table 1.3

Physical characteristics of the reaches in five case studies.

Case Study location	Number of Reaches	Total Reach length (km)	Average reach area (ha)	Median length (km)	95th percentile length (km)	5th percentile length (km)
Glenelg	53	1,056.38	2,919.80	10.94	70.79	0.23
Lachlan	502	5,218.16	6,101.23	1.65	51.95	0.26
Lower Murray	179	871.38	7,320	2.79	15.07	0.39
Mid Murray	75	1,045.89	5,075.69	6.68	50.82	0.35
Moonie	133	1,323.35	708	6.89	30.24	0.83

Table 1.4

Percentage of reaches within the catchment where connectivity occurred

Case Study	Driest Year			Wettest Year		
	Reach-Reach (%)	Reach-Waterbody (%)	Year	Reach-Reach	Reach-Waterbody	Year
Glenelg	44.69	0.13	2008	86.13	0.2	1992
Lachlan	65.81	1.71	2005	80.25	6.02	2012
Lower Murray	98.93	38.49	1998	100	79.73	1990
Mid Murray	91.09	19.12	1997	94.99	27.17	1996
Moonie	8.82	4.67	1992	32.75	26.85	2011

Table 1.5

RMSE and Nash-Sutcliffe model efficiency for station 412002 stream model (model 2 is a simple regression model between air and water temperature).

Model # parameter	RMSE (smaller is better)	NSE (1 is optimal)
2 = regression	2.27	0.77
3	2.14	0.80
4	2.08	0.81
5	2.04	0.82
7	1.39	0.91
8	1.38	0.92

Table 1.6

Percentile values of the first and last week of the entire time series where 80% of the reaches within a catchment are within the permissible range for virus activity.

Case Study	Winter - Summer (Week)			Summer – Winter (Week)		
	Median	20th percentile	80th percentile	Median	20th percentile	80th percentile
Glenelg	45	44	46	10	5	11
Lachlan	42	41	43	14	13	15
Lower Murray	39	39	40	17	17	18
Mid Murray	42	41	47	11	6	12
Moonie	46	37	48	14	10	18

Figures

Figure 1.1

The five catchments in South-East Australia included in the integrated hydrological study.

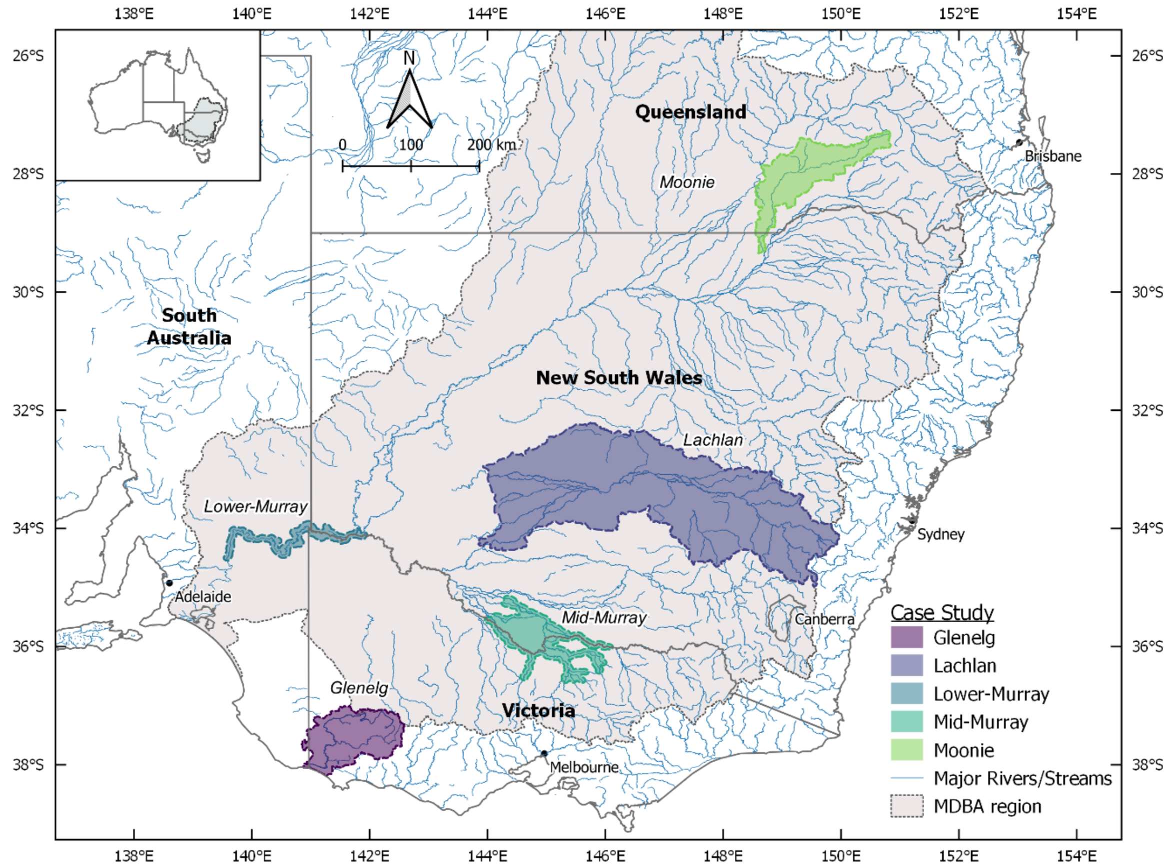


Figure 1.2

Validation plot showing flows at the upstream section of the Murray River (reach id 65) and the closest gauge data (409202).

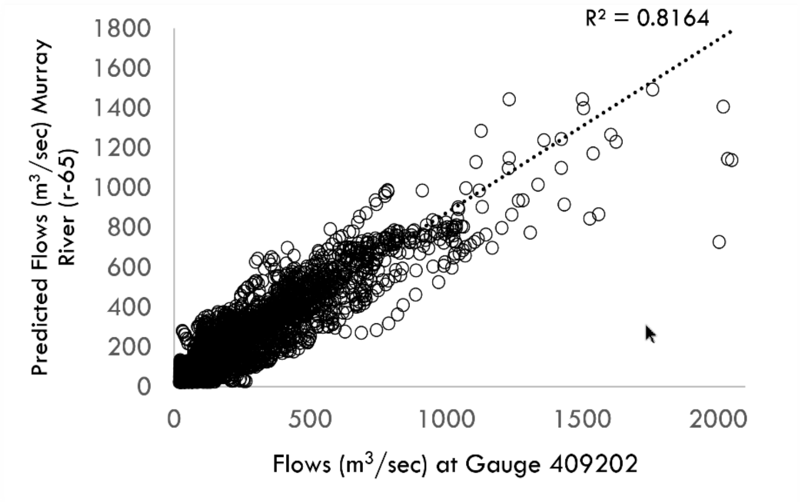
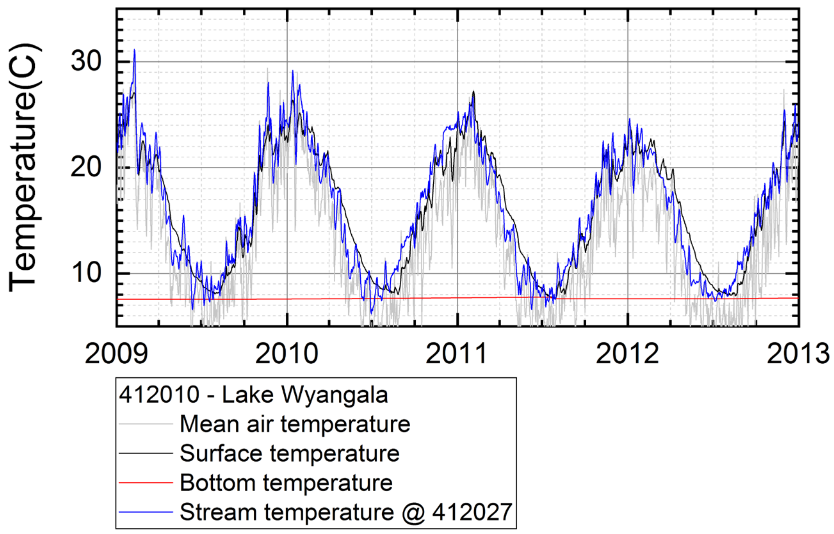


Figure 1.3

(a) Deep Lake Wyangala showing strong stratification (low bottom compared to surface temperature); (b) Shallow Lake Brewster showing weak stratification and frequent mixing (equal surface (black) and bottom (red) temperatures) with similar results for lake and stream model (blue). Grey line is air temperature

(a)



(b)

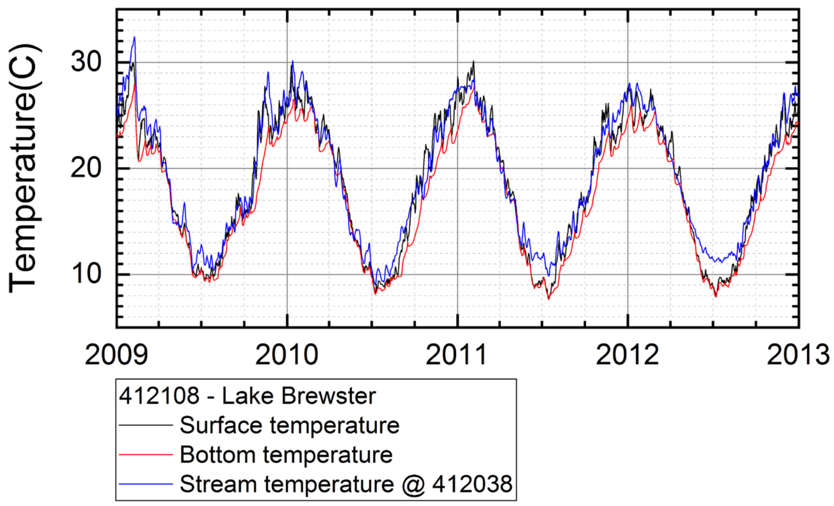


Figure 1.4

Observed and simulated stream temperatures using different model parameterizations and flow rate for station 412002 (Lachlan River at Corowa). Observations (black lines), simulations (coloured lines), air temperature (grey lines). Top panel is the entire simulation period followed by a 4 year section and a close view of the seasonal cycle in 2010/11. The bottom panel shows flow rates during this year.

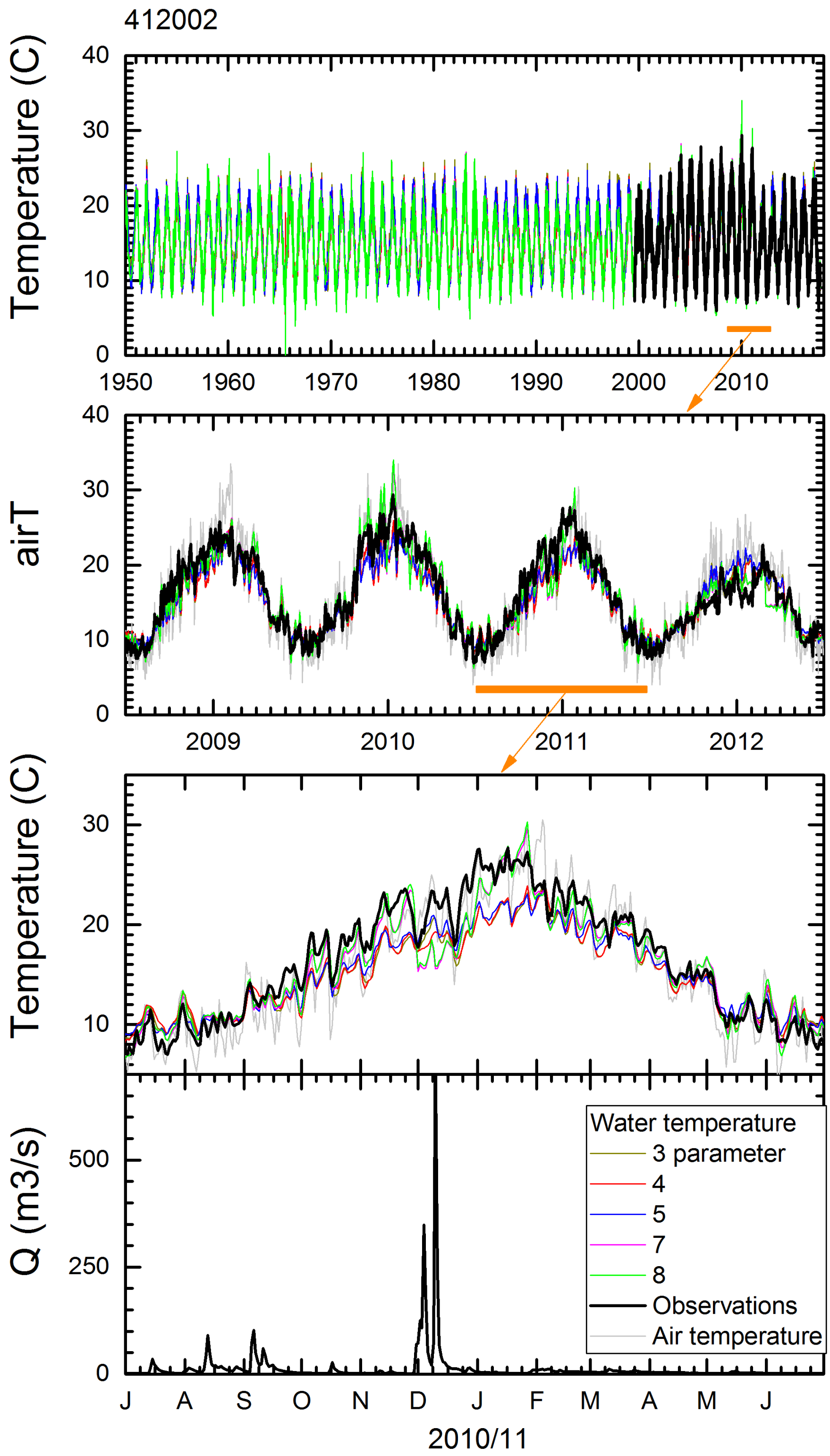


__Figure 1.5__

Comparison between observed water temperature (Station 4170204A at Fenton, Moonie) and simulated water temperatures using the stream model and no flow (purple) and the lake model (black).

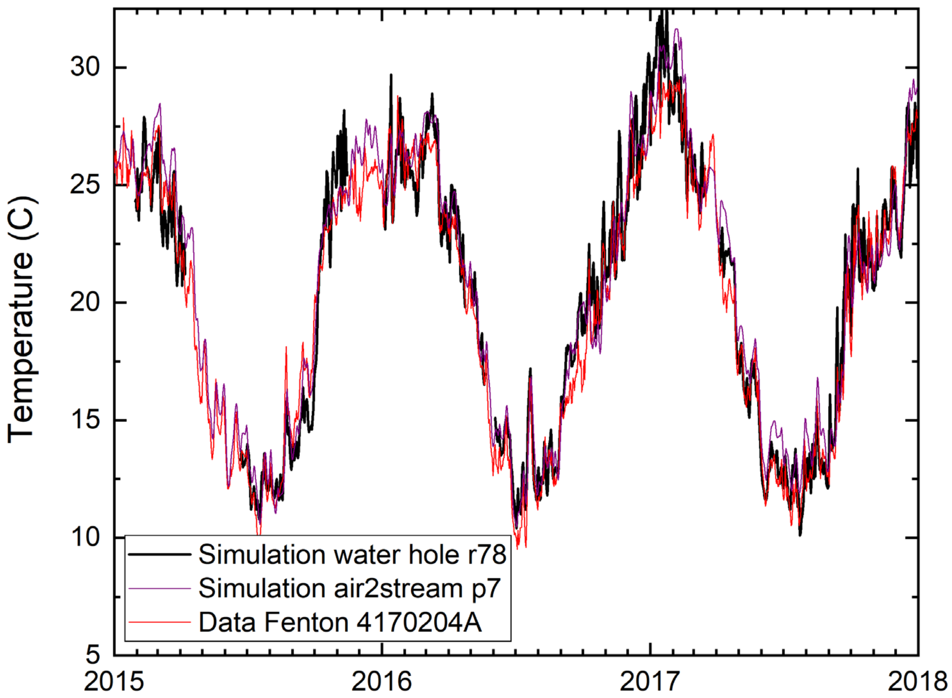
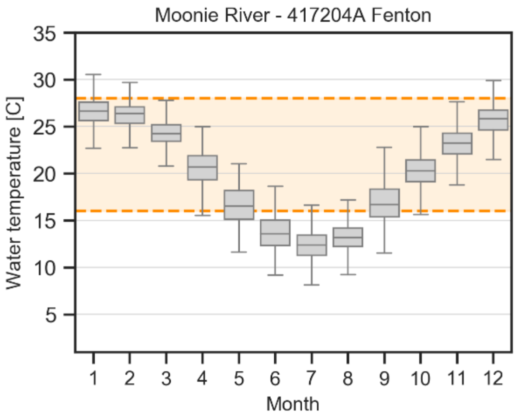


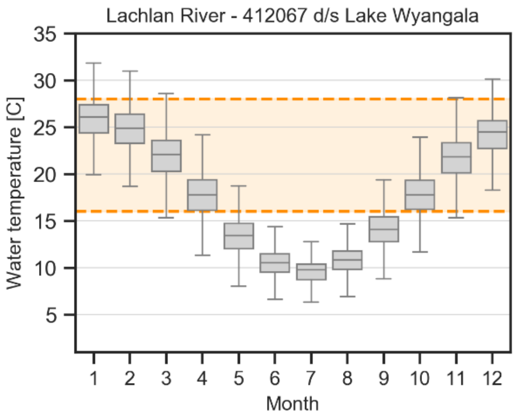
Figure 1.6

Monthly statistics of simulated water temperatures from 1990 until 2015/2018 in the 5 catchments from North to South. Overlay is a suggestive orange band of temperatures (16-28 C) for optimal virus activity.

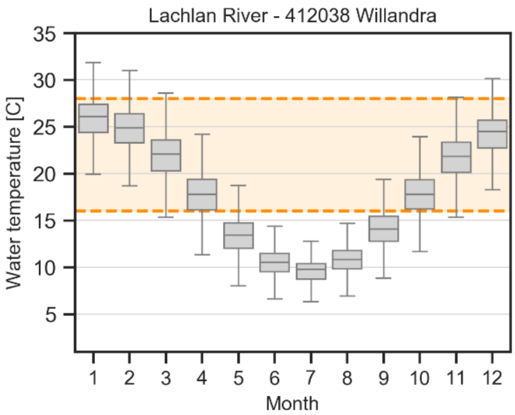
a)



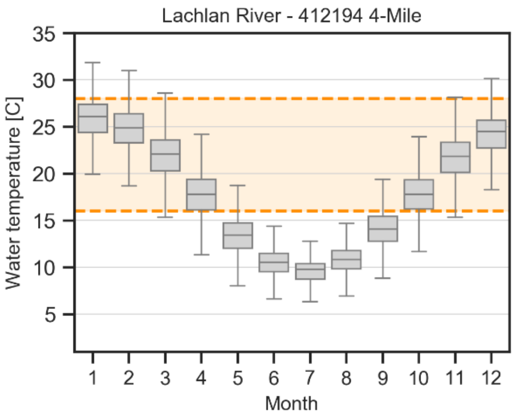
b)



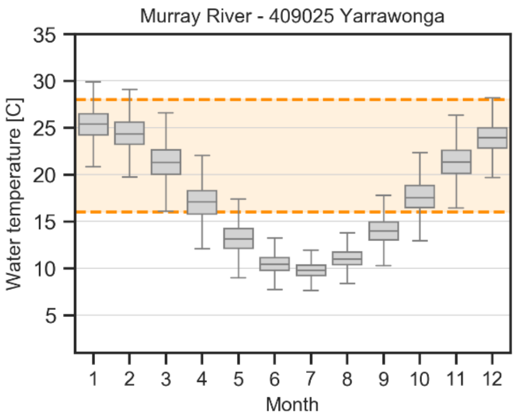
c)



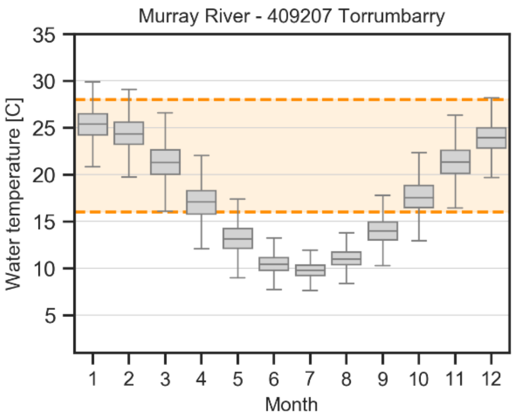
d)



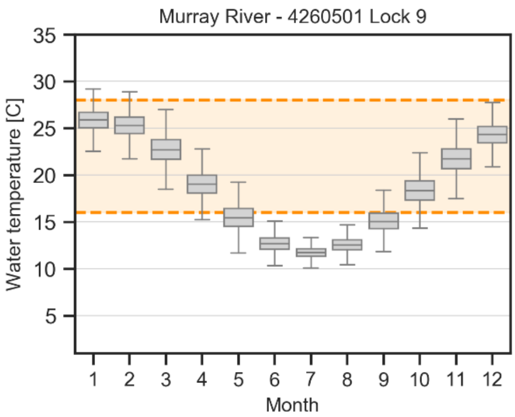
e)



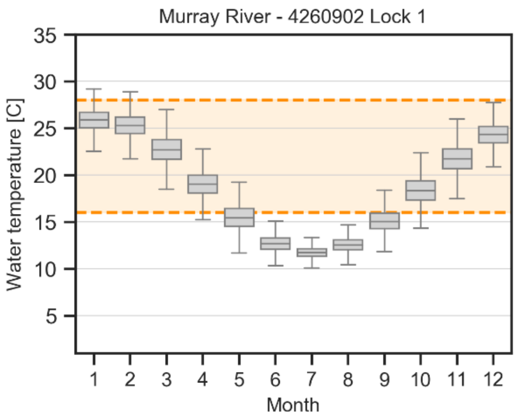
f)



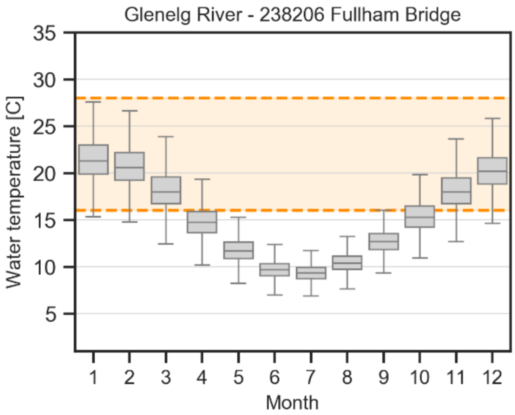
g)


Murray River - 4260501 Lock 9
Water temperature [C]
35
30
25
20
15
10
5
1 2 3 4 5 6 7 8 9 10 11 12
Month

h)


Murray River - 4260902 Lock 1
Water temperature [C]
35
30
25
20
15
10
5
1 2 3 4 5 6 7 8 9 10 11 12
Month

i)


Glenelg River - 238206 Fullham Bridge
Water temperature [C]
35
30
25
20
15
10
5
1 2 3 4 5 6 7 8 9 10 11 12
Month

j)

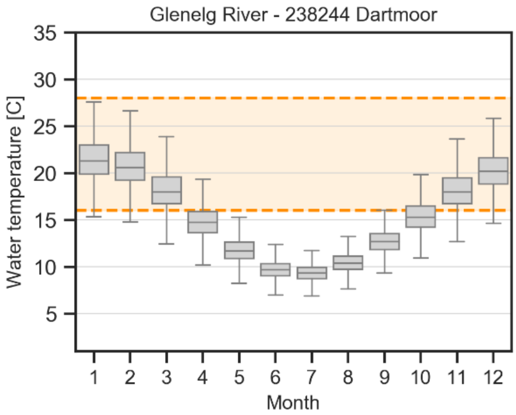

Glenelg River - 238244 Dartmoor
Water temperature [C]
35
30
25
20
15
10
5
1 2 3 4 5 6 7 8 9 10 11 12
Month

Figure 1.7

Annual cycles of number of reaches within the permissible temperature range for virus activity. Each line represents a single year. Red lines within the winter-summer period indicate the median first week over the entire time series where 80% of reaches are within the optimal permissive range and during the summer-winter period, the red line represents the last week where 80% of reaches are within the optimal permissive range. Orange lines represent the 20th and 80th percentiles for both spring and summer. For values see Table 6

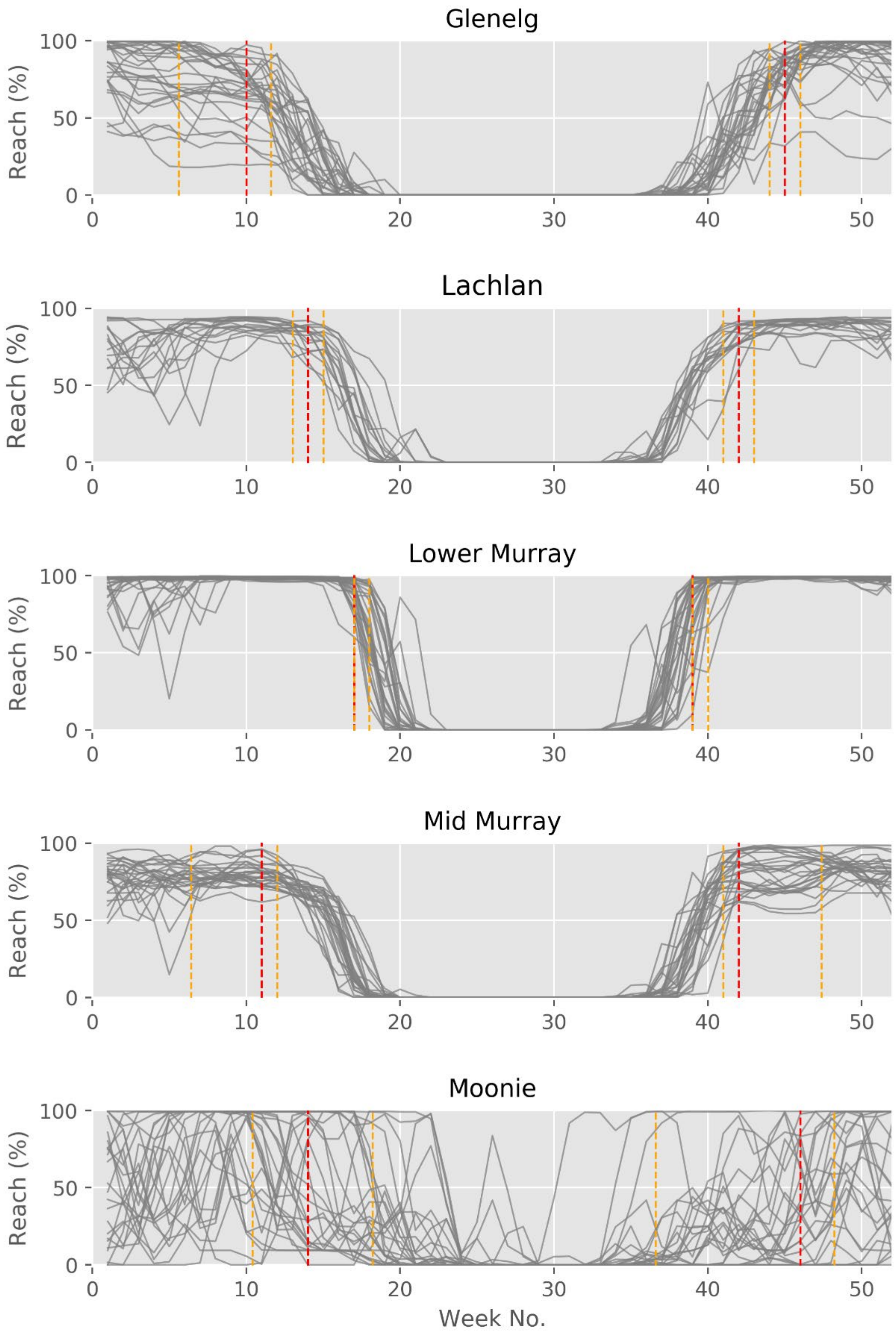


Figure 1.8

Percentage of reaches with water temperature in the permissible range of virus activity (green), below (light blue), above (red), and where no flow is present (yellow). Limited time-series data was available for the Lachlan and the Moonie catchments as shown in the missing grey regions.

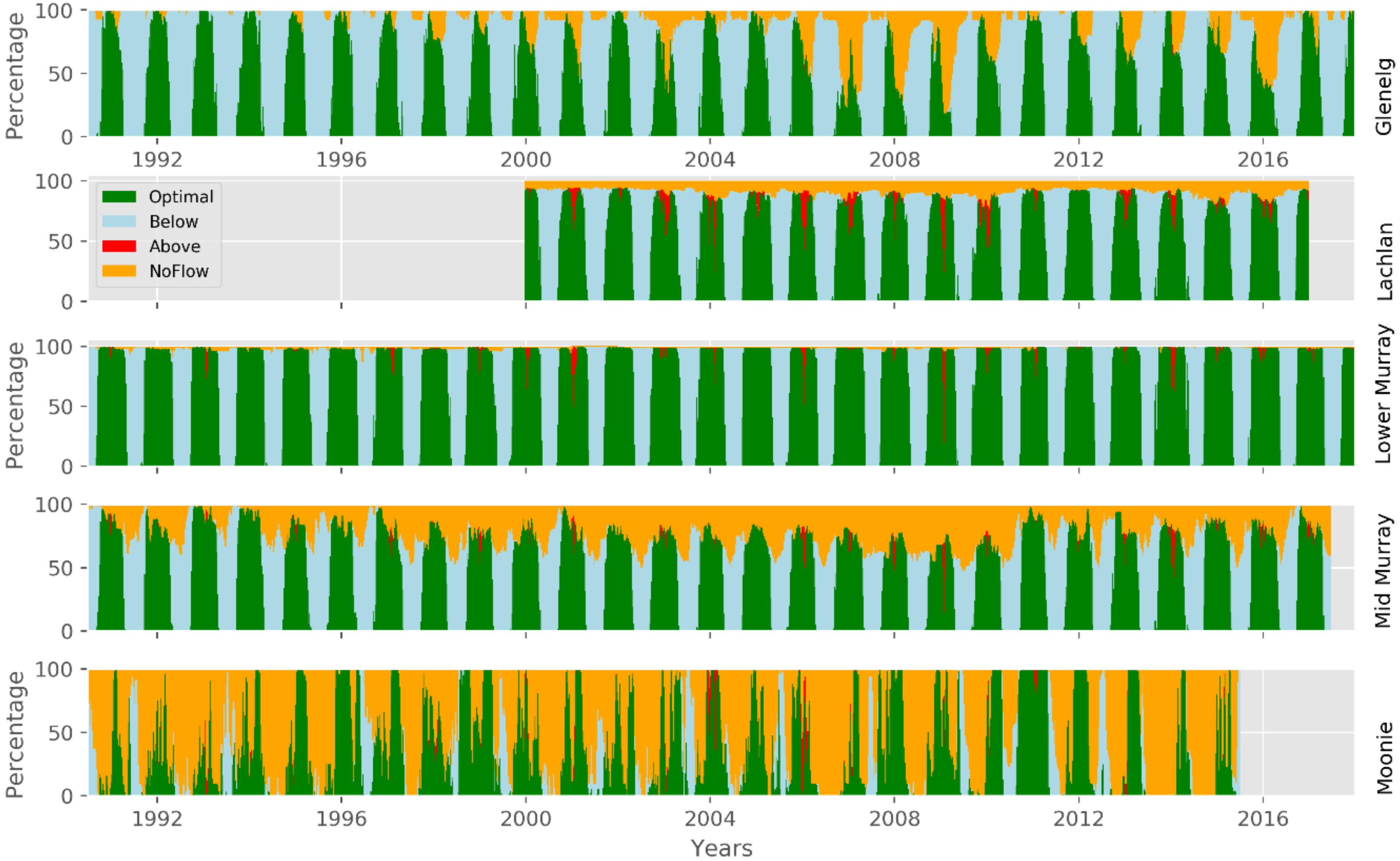
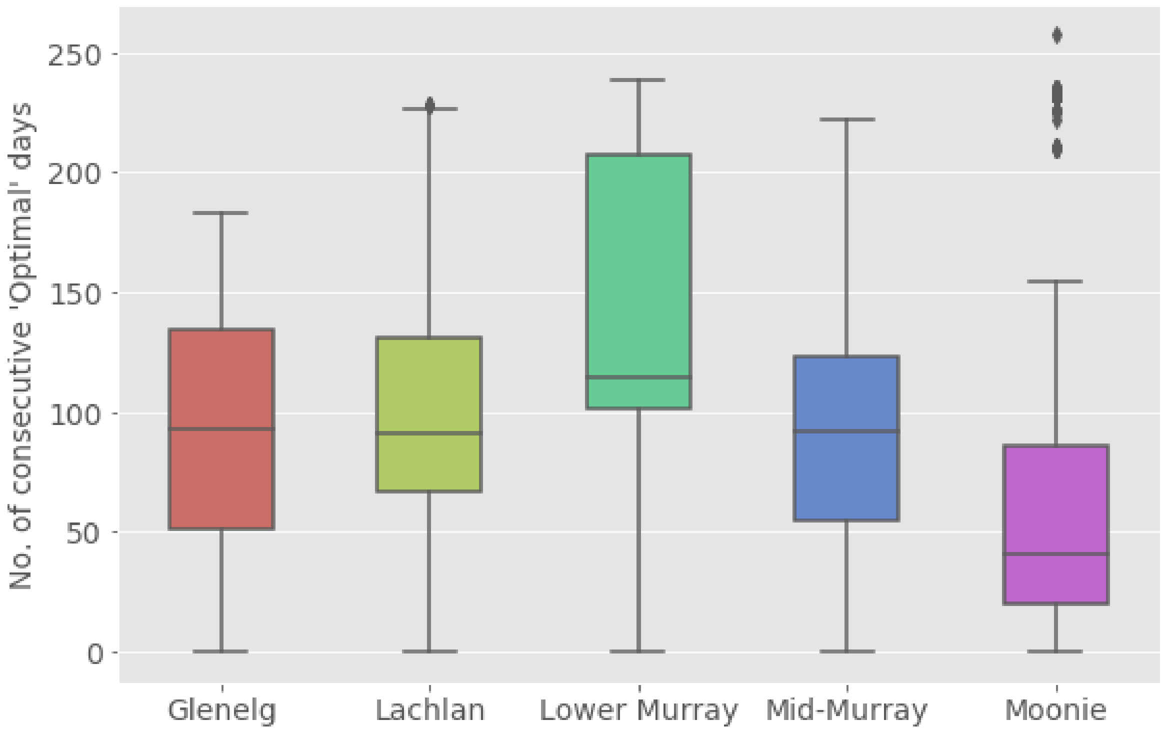


Figure 1 9

Summary box plot of the number of consecutive weeks with water temperature in the permissible range of virus activity.



Supplementary Material

S1 Description of selected catchments in south-east Australia

In the following we give a comprehensive overview of the five selected catchments.

Moonie River is an intermittent, dryland river in southwest Queensland, Australia, and a tributary of the Barwon River in the Murray Darling Basin. The river drains a total catchment area of 14,870 sq.km, with 10 primarily ephemeral tributaries. The river is a simple channel system with few tributaries with a series of waterholes which are connected for about one-third of the year. The catchment area is about 1.4% of the entire Basin which is sparsely populated with some agricultural demands. Thallon weir is the only significant storage in the system built to supply water to the town of Thallon, and there are major shallow and deep groundwater aquifers in the catchment. The catchments draining into the Moonie River and tributaries are relatively flat with the elevation changing from 1000-1250 m in the headwaters to 600 m above sea level in the lower portion of the catchment. Precipitation variability is low in the catchment with a mean annual rainfall that varies from 650 mm in the upper parts of the catchment to 450 mm in the lower parts. The pan evapotranspiration is high ranging between 1800 and 2200 mm year^{-1} and a mean daily maximum and minimum temperature of 27°C and 13°C (Balcombe et al., 2014). The hydrology of the system is dominated by rainfall-runoff interactions with nominal base-flow and groundwater interactions. The flows in the system, governed by the geography (low gradient) and climate (high temperature and evapotranspiration), are low with extended dry periods. During dry periods, disconnected waterholes serve as refugia for the aquatic biota, during the wet periods, the waterholes are connected providing the opportunity for the fish to migrate. The catchment is in natural and unregulated, except weirs and in the downstream reaches where flows are impacted by abstraction for irrigation purposes. The catchment sustains habitats for several protected species of birds and vegetation communities.

The Lachlan River catchment (~ 90,000 km^2) is located in central NSW and west of the Great Dividing Range. The catchment topography varies markedly from east to west from the hilly headwaters to very flat western regions characterised by a highly braided river network. The Lachlan catchment borders the Murrumbidgee catchment to the south and the Upper Darling and Macquarie catchments to the north. Although a tributary, very little water from the Lachlan River reaches past the Great Cumbung Swamp to the Murrumbidgee River except during major floods (MDBA, 2012). The Wyangala Dam (1.22 ML) is the main storage that regulates the flow along the Lachlan River. A number of natural lakes e.g. Lake Cargelligo (36,000 ML), Lake Brewster (154,000 ML) and Carcoar Dam (35,800 ML) have been modified to use as storages (NSW DPIE, 2019). There are several wetlands of national significance particularly as waterbird habitat. They include Lake Cowal near Forbes, Lake Brewster, Booligal wetlands and the Great Cumbung Swamp (NSW DPIE, 2019).

Mid-Murray region is approximately 3% of the Murray-Darling system with the river spanning over 1200 km from Hume Dam in the east to the confluence of the Murray and Darling Rivers at Wentworth in western New South Wales. Several rivers enter the Murray-Darling system making it hydrologically relevant. For the purpose of this study, the tributaries and the branches included are Tuppal Creek, Edward Creek, Wakool River, Tulla/ Budgee creeks, Broken Creek, Goulburn River, Gunbower Creek, and Campaspe River. The river is perennial in this region with extensive floodplains and wetlands of national and international significance, such as the Barmah-Millewa Forest and the Gunbower-Kondrook-Perricoota Forest. The floodplains are broad and flat with an intricate network of creeks, floodrunners and billabongs. The Mid-Murray region features a major anabranch and floodplain system, the Edward-Wakool, which supports a high proportion of native fish at all stages in their lifecycle including threatened species such as the Murray cod, trout cod, silver perch and Murray crayfish. It also provides refuge habitat during periods of drought. This region not only supports a vast range of plants, animal species and forests, water is diverted to provide waters for domestic use, and support agriculture, tourism and recreational activities. The drop in the elevation over the 1200km reach is less than 50m. Though the system is perennial, there is seasonality in the flows stemming from precipitation patterns. Rainfall predominately occurs in the winter and spring months, with a hot and dry summer. There is also some spatial variability observed with approximately 700mm of rainfall in the east and 300 mm in the west. Major storages and control structures include Mid-Murray storages, Yarrawonga, Torrumbarry and Mildura weirs.

Lower Murray extends from the confluence of the River Murray and the Darling River at Wentworth, New South Wales, to the Murray Mouth at Goolwa, in South Australia covering approximately 9% of the Murray-Darling system. The region in semi-arid and with significant wetlands including the Riverland wetland, Chowilla Floodplain, and the Coorong at Murray Mouth. The river flows about 530 km as a deep channel with flat and dry floodplains. The river splits into two large distinct channels, the lower Darling River, and the Great Darling Anabranch. While there are other tributaries such as Rufus River, Chowilla Creek and Pike River etc, only the Great Darling Anabranch is considered in this study. Lake Victoria is the biggest storage within the case study extents. The change in the elevation is less than 100m, which means that the flood peaks take a longer time to reach the lower Murray. The region has one of the lowest rainfalls (220-280mm) in New South Wales and combined with the low topographic gradient implies that the runoff to the channel is negligible. The river flows are impacted by seasonality, especially from storms and rainfalls in the northern and eastern catchments of the Northern Basin. While the region is sparsely populated there are some urban centers and land uses primarily include pastoral grazing, large dryland agriculture and horticulture.

Glenelg River is the largest in south-western Victoria and a perennial river system spanning over 500 kms with headwaters in the Grampian National Park to the Southern Ocean at Nelson in the south-west Victoria (Figure 1.1). The total catchment size is approximately 12,660 km^2 with Wannon River as the largest tributary in the system. It is an integral part of the Wimmera-Mallee waterway system which supplies to the communities in north-western region of Victoria. Moora Moora and Rocklands Reservoirs in the upper Glenelg catchment are used to divert water for anthropogenic uses. While the entire catchment has high ecological significance, the lower reaches are recognised as one of Australia's I5 national biodiversity hotspots. Flows in the system is expected to cease between February and April but alterations in the system impact the natural flow regime. Currently, January to April are the low flow months with transitions during the month of May to June, and high flows are observed during the months of July to October. November to December are the transitional months. A 2003 study concluded that the streamflows in the system is lower than expected under natural flow regime in the main stem of the Glenelg River. Rockland Reservoir impacts the flow in the system considerably reducing the frequency of large flow events. The river system has isolated connections to the groundwater table in the area.

S2 Standardised reaches and waterways of the 5 catchments

The reach structure used in our simulation study is shown in Figure S1 for all five catchments

S3 River flow modelling

This section gives an extended description of flow modelling for the five catchments.

Moonie

The Queensland Govt. provided flow data for the Moonie River System over the period 1990-2015. These flows are a combination of observed flows and three models developed for the main stem of Moonie River. First two models, rainfall-runoff model (Sacramento model) and IQQM were developed in tandem with the Sacramento model used to fill data gaps in the observed flows. Finally, an upgraded Source models was developed to include the lower Fenton gauge. Typically, it has been observed that the storages and the waterholes have a minimal effect on the calibration of the model. While the storages primarily fill due to lateral runoff from the catchments, a 10% headwater and 25% residual inflow is set to pass through the storages from the reaches. These proportions are based on a catchment area vs. storage volume linear relationship developed after a sensitivity analysis was conducted at the data collection stage. The model assumes losses from evaporation occurs from the storages and the waterholes but there is no direct rainfall input to them. The compensation flows from the reaches and runoff account for the difference between storage inflows and outflows so when a storage is full any additional inflow other than the upstream flow (i.e. rainfall) becomes extra overflow and adds volume to the downstream flows causing a change in the mass balance. When rainfall on the storage is ignored this will not occur. The model was run with the upstream and residual inflows (in the proportions applicable) and the storages and waterholes included. The flow losses due to the storages collecting water were calculated by subtracting the flow downstream of the storage from the flow upstream. This was done for different time periods each with a different percentage of the storages active, and with the waterholes always 100% active as they are/have been always there. A completed storage loss file was manually pieced together from the runs from the different time periods to produce a continuous IQQM storage loss file that ran for the full period. The main stem of the Moonie was defined either as headwater reaches or residual reaches using gauging station and the nearest upstream gauging stations. However, these flows were available typically for the gauges on the main stem of Moonie and no flows were available for the sub-reaches delineated specifically for this study or any of the tributaries to the main stem.

The Moonie system was split in four main reaches based on the location of 4 major stream gauges that were selected based on the reliability and the quality of the data. SILO daily rainfall data was obtained from the 12 rainfall stations maintained by the Bureau of Meteorology. Finally, the evaporation data was obtained from the meteorological data stored in the SILO drill dataset. Detailed modelling activities is described in the Queensland Govt. Modelling report.

Streamflow records for the Moonie River are available typically for at least a decade from gauging stations at Nindigully and Fenton in Queensland and Gundablouie in New South Wales. Historical and current extractions to meet anthropogenic demands are assumed to be minimal based on data currently available. To predict flows in the sub-reaches, a new rational method based modified model was developed using the modelled and observed flows provided by the Queensland Government. Rational method is one of the simplest methods to estimate the discharge from a drainage basin runoff. The runoff equation estimates discharge based on a runoff coefficient (estimated from land use) and the total drainage area and the rainfall intensity. Landuse in the catchment is largely grazing and dryland cropping, with a small amount of irrigated agriculture (cotton and pastures). The flows were estimated for 61 subreaches in the main stem and the tributaries. Table S1 summarizes the number of catchments that contribute flows to the four gauges used in the model.

The runoff coefficient for pastures based on literature is in the range of 0.1-0.6. For this study, since the landuse and the rainfall is fairly homogenous, we estimated the fraction (Ci) from the gauged data and total area contributing to the gauge. The fraction is then multiplied with the relevant portion of the subcatchment area that contributes flows to the specific reach.

$Q=CiA$

Where, Q is discharge, C is the runoff coefficient, A is the contributing area of the sub-catchment, and i is the intensity of rainfall.

In the headwater reaches, flows are generated only from the runoff in the contributing catchment, and in the residual reaches, the flows are an accumulation of the headwater flows and the runoff from the catchment delineated for that specific reach. As described above in table S1, we use streamflow data from the four gauges to benchmark the flows estimated in this study. At each gage the predicted flows were validated with the gauge data and the flows provided by the IQQM model. Due to lack of gauges the flows there are not validated in the tributaries.

Lachlan

There are more than 60 streamflow gauging stations in the catchment with streamflow data ranging from less than a year to around 18 years since January 2000. The data gaps also vary from almost none to 100% data missing, i.e. some of the stations listed in the NSW Water Information data portal (http://waterinfo.nsw.gov.au/) have no data.

Surface water flow estimation of the Lachlan River and its tributaries was derived based on a combination of flow values derived from three sources:

- Australian Water Resources Assessment (AWRA) output;
- GR4J hydrological model (Perrin et al., 2003); and
- NSW Government's observed data.

The AWRA modelling results from the Water Information Research and Development Alliance (WIRADA) - established between the Bureau of Meteorology and CSIRO (BOM, 2016) - were used to determine gap free stream flows necessary to drive water temperature and demographic modelling. The AWRA comprises landscape (AWRA-L) and river (AWRA-R) models (Vaze et al., 2013). AWRA modelled data is available for 41 stations from 1970 to mid-2014 resulting in gap free 'observed' data for this period obtained by patching the missing data with the modelled data. Data from mid-2014 to September 2017 for 24 gauging stations was obtained from observed record, while 17 of the stations have no observed data for this period. The use of AWRA as basic data source was favoured at this stage as it is available for many catchments in Australia. However, it might miss the rigour of accounting for all kinds of linkages and operational rules as would be possible in a fully implemented eWater Source model, which on the other side is not or not yet available for most catchments.

The GR4J rainfall-runoff model (Perrin et al., 2003) was used to determine streamflows in headwater catchments where both the AWRA and the observed gauging stations data were unavailable. GR4J uses daily observed precipitation (P) and potential evapotranspiration (E) as input which were obtained from the SILO Data Drill (www.longpaddock.qld.gov.au/silo; Jeffrey et al. (2001)). GR4J has been widely used in Europe and Australia. Depending on the hydrological processes to be simulated, four or more parameters are used. For this study we used four parameters: x1, x2, x3 and x4. These parameters represent: two different storages (x1 and x3), lag(x4) and groundwater exchange (x2). The GR4J was coded for this project in MATLAB based on the algorithm given in Perrin et al. (2003) and were tested with data and results from an earlier study. The model was calibrated using automatic optimisation technique for the Boorowa River headwater catchment (412029). The optimised model parameters were then transferred to other headwater catchments representing upstream of Links 70 (upstream of Lake Cowal), 6, 20, 97, 132 and 135.

Since the Lachlan River network is highly braided downstream of Forbes with partly not well-defined flow paths, streamflow estimation for ungauged or unmodelled links were done using a number of techniques. These include linear regression, division of flow at a fork based on a given proportion, linear interpolation (Jeffrey et al., 2001), flow addition/subtraction and based on previous to next day's flow ratio at a nearby link.

Estimation of surface water flows for all tributaries of the Lachlan River is challenging given the sparseness of the streamflow gauging stations and highly braided stream network. Modelled or gauged streamflow data are not available for all reaches in the catchment where streamflow estimation is needed, therefore the confidence in estimated flow varies from reach to reach.

Mid and Lower Murray

The mid-Murray system has been extensively studied and a number of models exist for this region. One example is the MIKE 21 model for the River Murray Channel environmental water requirement for ecological objectives developed by the Goyder Institute. However, the most relevant and up to date model is the eWater Source model developed and maintained by the Murray-Darling Basin Authority. This integrated river system modelling framework links the existing state models. The model is calibrated and validated at a daily time step, and the model functionality accounts for the interstate water sharing arrangements, and individual water sharing plans. The model represents the demands and delivery of water for the environment. Model's functionality meets the accountability and it is deemed 'fit for purpose'. The model is configured for a baseline diversion scenario and runs for a period of 114 years. Though the gauge network is extensive in the Mid-Murray, it is not sufficient for defining flows in the sub-reaches required for carp movement and habitat. There are two primary reasons for not relying on the gauge data, first, flow data in many of the gauges are not long enough, and second, without detailed knowledge of water sharing and abstractions, flows allocations to the sub-reaches can be erroneous.

While eWater Source model exists for the Lower Murray system, reliable observed daily flow data was available enabling estimation of flow data by sub-reaches for this part of the catchment. The flows for partial Lower Murray (Locks 1-6) was provided by the Department for Environment and Water, and for the remaining (Locks 7-10), data was downloaded, and gap filled.

While there are no public available models for the Glenelg system, there do exist models and associated reports. A 2009 assessment conducted for the Victorian Environmental Flows Monitoring and Assessment Program (VEFMAP) led to the development to a series of one-dimension and two-dimensional hydraulic models. Similar to the Lower Murray, daily flows in the main stem and the 5 tributaries were estimated via a reliable network of gauges. Missing data was filled in by interpolation. In case of no gauges in a given sub-reach, data from the closest upstream gauges and any inflows from tributaries were used to estimate the flows. These flows were then cross-checked against the downstream gauges.

For Mid-Murray system, the eWater source model calibrated and validated by the MDBA was used to predict flows in the subreaches. The baseline scenario for this run of the model assumes a 2009 level of development and all diversions in the system are accounted for. The modelled data was validated against gaged data.

In the Lower Murray, daily flow volumes over Locks 1 through 6 are estimated using upstream and downstream water levels and 'accounts' of the crest level of segments of the weir structure. Flow data is calculated using the QLock application, which uses water level and weir flow formulae to produce estimated total flow over the weir. No allowance is made for water passing downstream via operations of the lock chamber (Stace, 2008). Flow data was exported from South Australia's hydrological database, Hydstra. Daily flow to South Australia (QSA) was exported from the Hydstra database. Data gaps in the flow records were patched using linear extrapolation when missing data was less than three consecutive days. The data record was extended from 05/06/2018 to 30/06/2018 using QSA data exported from the Murray Darling Basin Authority website (https://riverdata.mdba.gov.au/flow-south-australia-calculated). In addition, a modified version of the eWater Source Murray Model (MDBA, 2019) was used to generate the modelled estimates at lock sites where data patching was required.

Daily flow data was not available for every monitoring location and data patching was required at all lock sites to complete the record. Missing daily data (QLock) was patched with modelled data outputs in all instances for Locks 1, 2, 3, 5, and 6. This included the period of record where data appeared to be anomalous during times of peak flow, where water levels exceeded the specifications of the site and QLock was unable to accurately calculate discharge. Daily flow over Lock 4 was patched with flow volume from the upstream gauging station at Lyrup (A4260663) where applicable. However, data from the Lyrup gauging station was not always of suitable quality and was also patched using model outputs. Modelled data was used to estimate flows at the Chowilla downstream of regulator storage between 01/07/1990 and 12/05/2017. The remaining data was patched using a lock flow data, where flow from the Chowilla Creek was assumed to be equal to the flow at Lock 5 minus the flow at Lock 6. For Locks 7 and 8, data was downloaded from BOM data online and SA WaterConnect and merged, the missing data was then patched with a simple linear regression using Python's StatsModel package. For Locks 9 and 10, data was only available from the BOM database, and the missing data was gap-filled using a polynomial second order interpolation using Pandas forward filling method in Python. The BOM gauges for the Great Darling Anabranch have no flows allocated, however, the WaterNSW Real time data had over 10,000 valid records, and the missing data was filled using polynomial second order interpolation using Pandas forward filling method in Python.

Glenelg

For estimating flows in the main reach of the Glenelg River and the 5 tributaries, we used the flow data downloaded from the Bureau of Metrology (BOM), with gap filling using data from the Department of Environment and Primary Industries, State Government of Victoria. Daily flows in the main stem and the 5 tributaries were estimated via a reliable network of gauges. Missing data was filled in by interpolation. In case of no gauges in a given sub-reach, data from the closest upstream gauges and any inflows from tributaries were used to estimate the flows. These flows were then cross-checked against the downstream gauges.

S4 Inundation modelling

This section gives an extended description of the inundation models used in the project. This is summarized in the main text.

Open Water Likelihood (OWL)

The OWL algorithm (Ticehurst et al., 2014) consists of five water-sensitive parameters. These are two Short-Wave Infrared (SWIR) bands, the Normalized Difference Vegetation Index (NDVI; Townshend and Justice (1986)), the Normalized Difference Water Index (NDWI; Gao (1996)) and the Multi-resolution Valley Bottom Flatness (MrVBF; Gallant and Dowling (2003)). It has been calibrated and optimized by Guerschman et al. (2011) based on its performance in the Australia continent. Its merit lies in the consistent performance over image time series, which means a unique cut-off threshold on whole time series can be applied to derive coherent inundation results, although it overestimates the amount of surface water in shaded slopes and misclassifies black soils as open water. Previous studies in the Murray-Darling Basin (Chen et al., 2012; Chen et al., 2013; Chen et al., 2015; Chen et al., 2014; Huang et al., 2014) have demonstrated that inundation extents detected from time-series of MODIS imagery using the OWL index have a high accuracy and strong stability, and a universal threshold is applicable to automatically delineate inundation extent.

OWL values delineate the probability of the existence of standing water within a MODIS 500 m pixel. The pixel values of the OWL images range from 0 to 100%, which can be interpreted spatially as no inundation within the pixel area (OWL = 0) to inundation occurrence over the entire pixel area (OWL = 100%). Using a suitable cut-off threshold, inundation extent can be derived from OWL images, which means a pixel with an OWL index greater than the threshold is classified as an inundated pixel, and vice versa.

RiM-FIM

In the lower Murray and the mid Murray case studies the RiM-FIM (River Murray Flood Inundation Model) products (Cuddy et al., 2012; Overton et al., 2010; Sims et al., 2014) were also used to establish areas of inundation.

RiM-FIM divides floodplains along Murray River, Edward-Wakool River, Lower Murrumbidgee River and Lower Darling River into 34 zones. It links measurements of water height at flow gauges to the extent of inundation mapped from Landsat TM images and interpolates the distribution (extent and depth) of inundation across the landscape using a Lidar digital elevation model (DEM). RiM-FIM enables the distribution of inundation to be predicted at 5 m spatial resolution over large areas, and at flow levels that were not observed in the Landsat images. The model shows flood extent at 1GL increments (Figure S2) in total daily flow ranging from the smallest flood shown in the images to the largest recorded flow with a measured height (Sims et al., 2014). RiM-FIM has been used by the Murray Darling Basin Authority (MDBA) when planning and implementing the Basin Plan. At the heart of the Basin Plan is the establishment of environmentally sustainable levels of take, which requires a spatial model linking river flows to the extent and depth of inundation.

Inundation modelling estimates

Modelling inundation extent using MODIS OWL model was conducted by firstly calculating an OWL index and applying a threshold value of 9% to each image in the time series from 2000 to 2018. The resultant MOSIS OWL images represent daily maximum inundation extent with OWL values ranging from 0 to 1 (1 is inundation with OWL $\geq$ 10%, and 0 is non-inundation with OWL < 10%). From the beginning of each year, every seven OWL images (except for the last week in the year) were then overlaid, a maximum OWL value among the overlaid pixels of the seven images was extracted. A total of 52 images showing maximum inundation areas were finally aggregated to weekly inundation extent maps for each year (Figure S3).

Mapping weekly maximum inundation extent from RiM-FIM was performed by extracting daily inundating extents from RiM-FIM products corresponding to an observed daily flow from a selected gauge station in selected catchments, and then aggregating daily extent to a weekly maximum area. In determining the weekly area of individual waterbodies, a bespoke Python script was created to compute the estimated area of inundation. This script takes the bounding area of the waterbody and assesses the area based on either the RiM-FIM commencement to fill values for the given week, or the recorded weekly inundation from Landsat imagery or MODIS OWL maps, whichever was applicable depending on the timing.

Evaluation of MODIS-derived inundation extent

Direct comparisons between inundation extent maps derived from MODIS OWL and Landsat TM images can be found from Chen et al. (2013) and Huang et al. (2014). In this study, MODIS-derived weekly maximum inundation extent was evaluated against RiMFIM-derived weekly inundation extent in Chowilla Riverland Floodplain (Figure S4). Figure S5 shows the comparison results of an OWL (Open Water Likelihood) image and a RiM-FIM map. The assessment (Table S2) indicates that the results provide a reasonable accuracy at the catchment scale to serve the purpose of guiding CyHV-3 release. A higher accuracy can be achieved for larger targeted flood events than smaller flows. The study also suggests that cautions need to be taken when selecting a threshold value because the cut-off points to distinguish water bodies and inundated areas from others may lead to over-estimation (commission error) or under-estimation (omission error) of inundation areas to some degree.

S5 Water temperature modelling

Water temperature models using air2stream usually performed best with full parameterization (p=8). However, in cases of no flow the model internally breaks down dividing by a zero flow value. This then results in unrealistic flow values as exemplified for station 412194 (Figure S6). These models were subsequentially disregarded.

The Moonie River is a specific type of river catchment, consisting of a string of waterholes connected via the river in case of flow. To take this into account a series of 15 waterholes (Table S3) were simulated using the lake model to compare with the stream model for simulate water temperatures. A main difference between waterholes is their bathymetry which influences heat distribution through changes in volumes related to area at depths. Hypsometric curves are shown in Figure S7 (data supplied by J. Marshall, pers. comm.). The model was calibrated using measurements for the Brenda waterhole resulting in a good match between simulated and measured surface as well as bottom temperatures (Figure S8). Simulations for the Moonie waterholes using this calibrated model show general consistencies in the surface water temperatures, while simulated bottom temperatures vary strongly across the waterholes (Figure S9) mainly due to differences in hypsometry and meteorological drivers are similar between locations. Simulations also showed a significant dependence of stratification and thus bottom temperatures on assumed turbulent background diffusivity. The stratification simulated here might change depending on slight variations in local wind conditions not matched by the smoothed, gridded wind data used in the simulation or turbulence generated by e.g. shear stress. Therefore, we can conclude that surface temperatures are a good representation of the actual situation for these waterholes, while bottom temperatures might differ to some extend from those simulated here depending on local peculiarities (wind, shading, small flows, etc.).

Supplementary Tables

Table S1

Number of sub-catchments by gauges.

Gauge	Number of Subcatchments
GS 417205a Moonie River at Flinton	26
GS 417201b Moonie River at Nindigully	13
GS 417204a Moonie River at Fenton	1
GS 417001 Moonie River at Gundabloui	2

Table S2

Summary of comparison results of weekly maximum inundation extent (MODIS vs. Landsat).

Inundation	**Overall accuracy (%)**	**Omission (%)**	**Commission (%)**
Weekly (OWL>1)	84.0	6.1	9.9
Weekly (OWL≥10)	88.8	8.5	2.7

Table S3

Waterholes in the Moonie River catchment for which a lake model was applied.

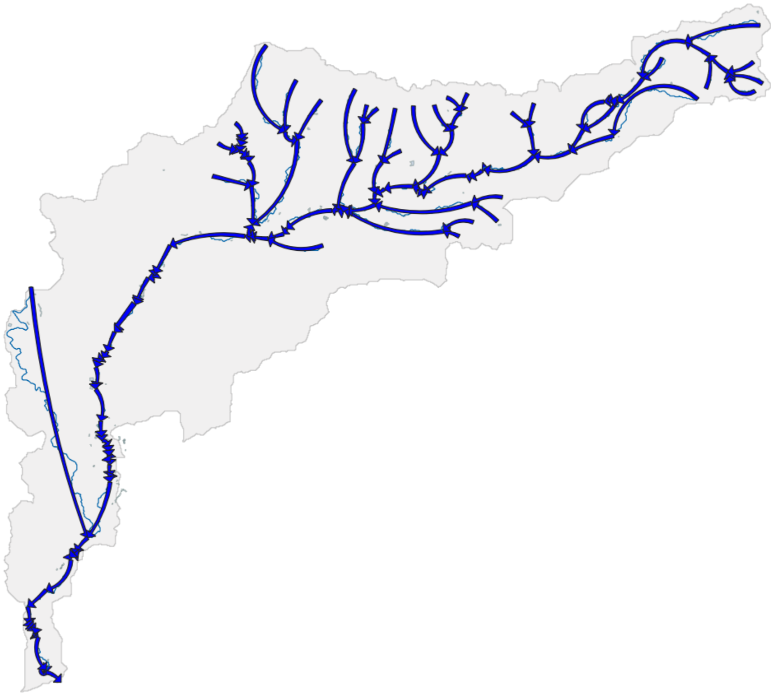
	Latitude	Longitude	Name
4170220	-28.64423022000	148.85388734400	-
4172008	-28.55526570400	148.83183244600	Bullamon Plains
4172009	-28.25802046610	148.87356538100	Kurrajong
4172010	-28.32829727170	148.84084264200	Appletree
4172011	-28.62649098680	148.85092074300	Broadwater
4172016	-28.08620387920	148.99347040500	Warrie 1
4172017	-27.89495392590	149.55993761300	Verena
4172018	-27.95591194700	149.38347005000	Kooroon
4172019	-28.17456658100	148.93763158900	Carbeen
417201A	-28.35183901150	148.81665320000	Nindi Pub
417201B	-28.42934588980	148.81603235500	Nindigully
4172020	-28.09636076780	148.98045323200	Warrie 2
4172021	-27.97124208810	149.27719863400	Altonvale
4172022	-27.78750125760	149.95721847100	Kurmala
417204A	-28.93119419020	148.73860339700	Fenton
422015	-29.02880000000	147.26560000000	Brenda

Supplementary Figures

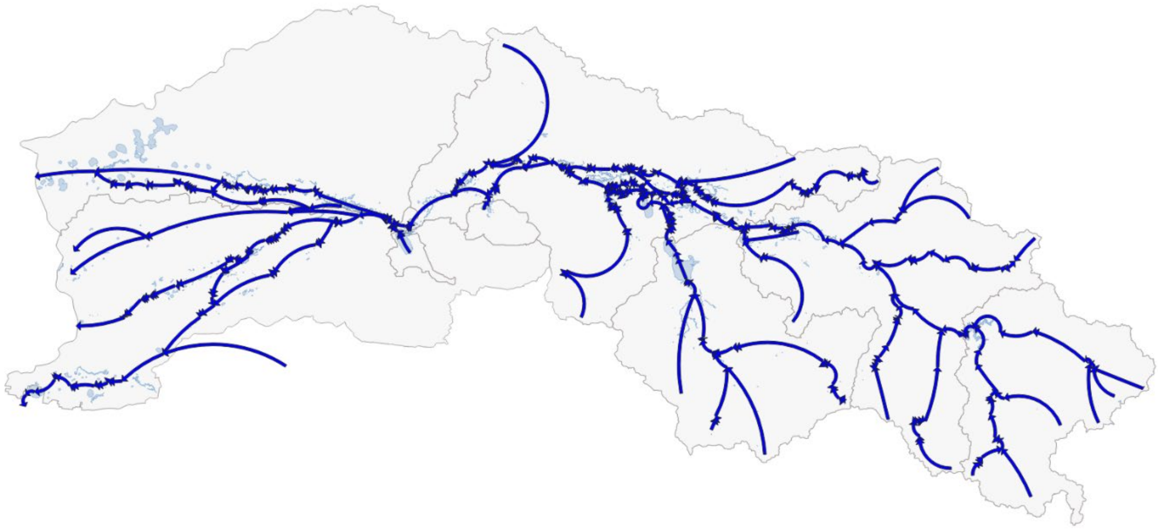
Figure S1

Reach structure in the five catchments (not to scale).

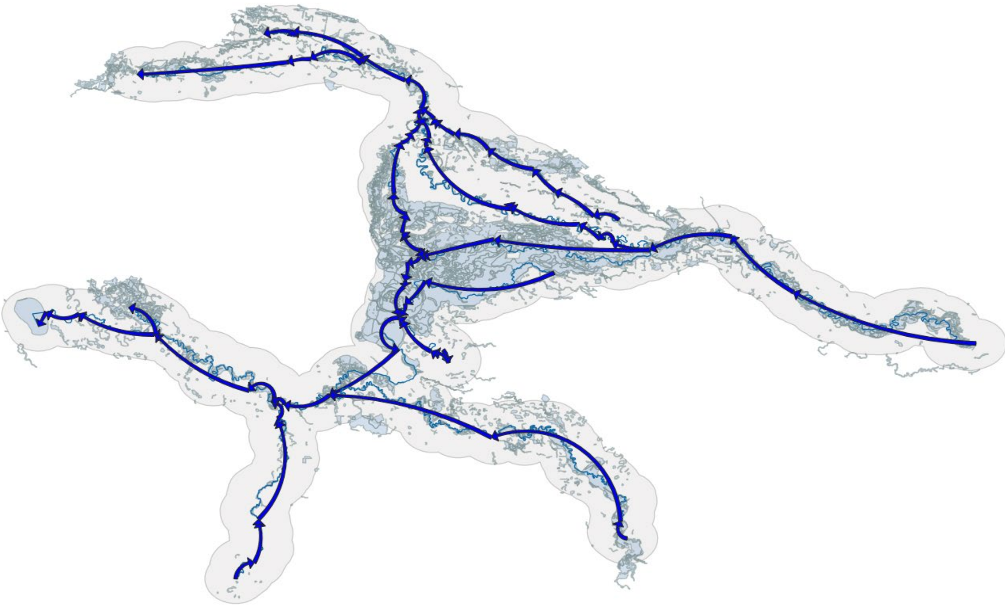
a) Moonie



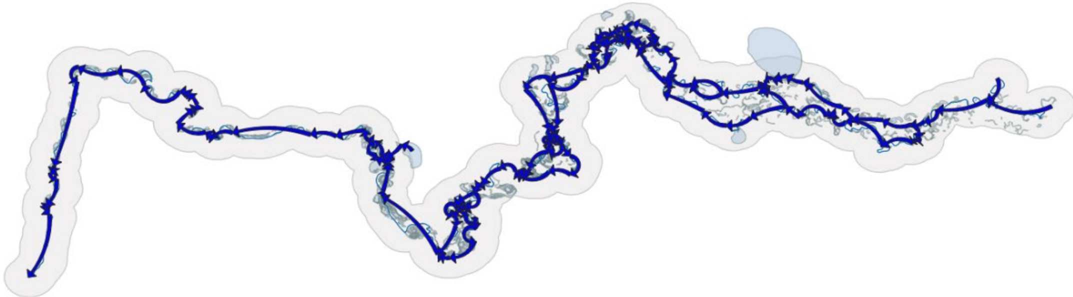
b) Lachlan



c) Mid Murray



d) Lower Murray



e) Glenelg

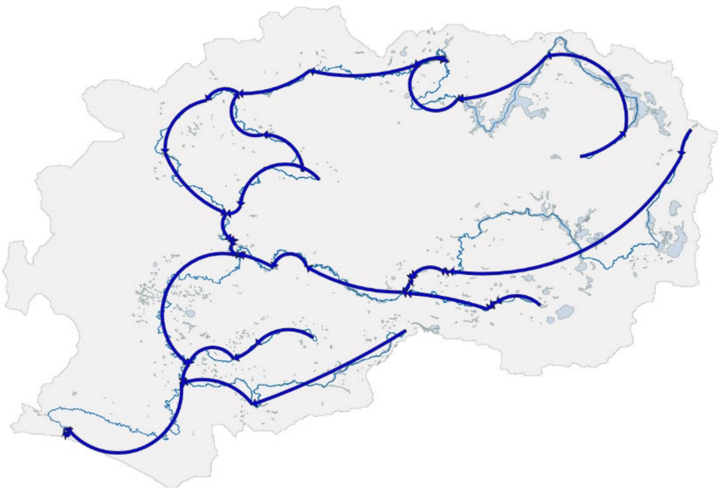


Figure S2

RiM-FIM example (left) and product coverage (right).

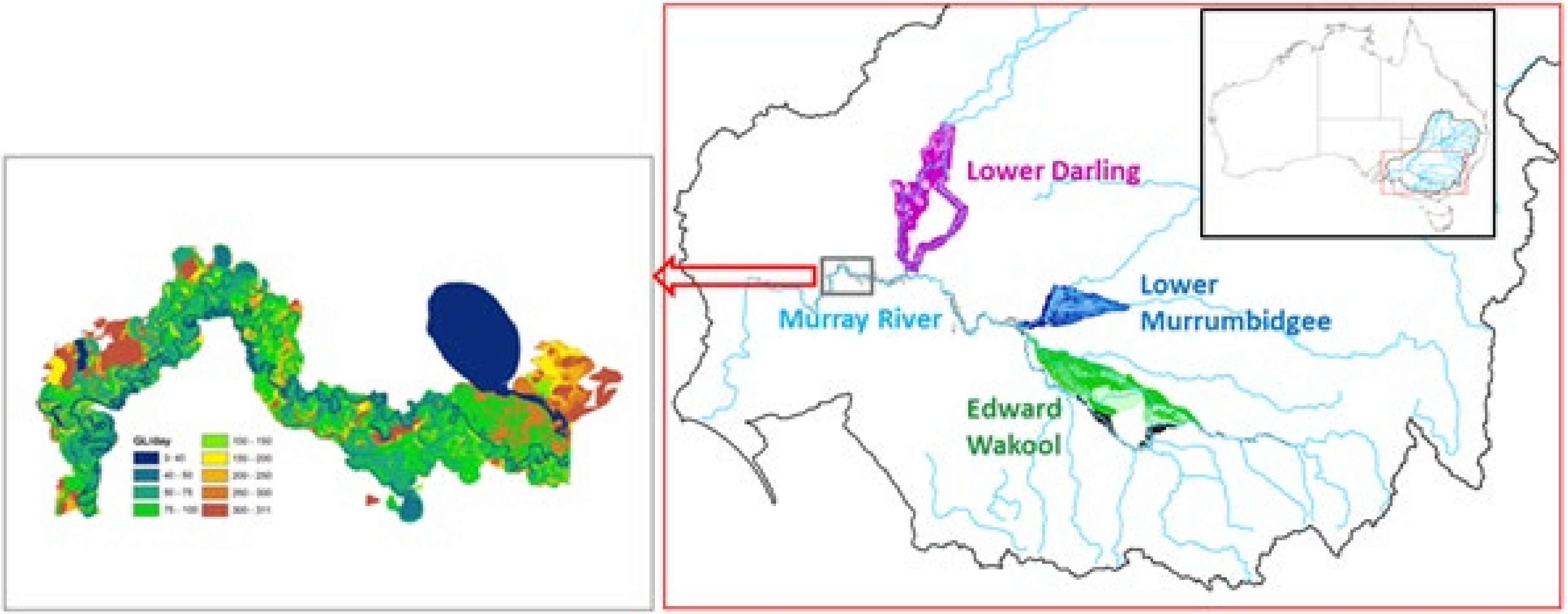
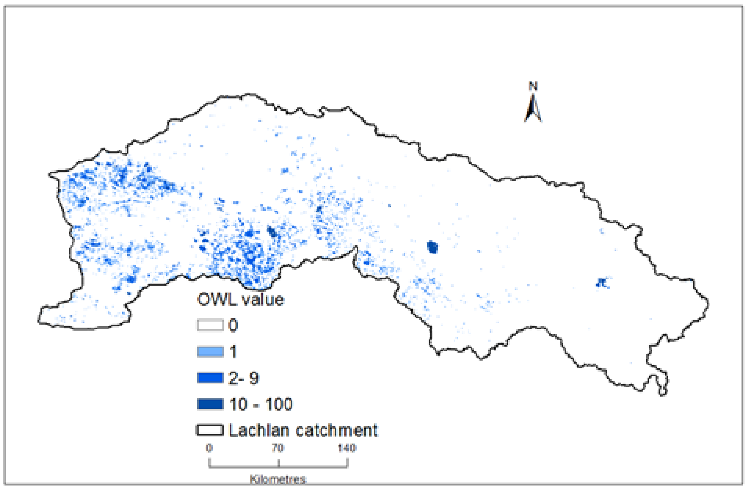


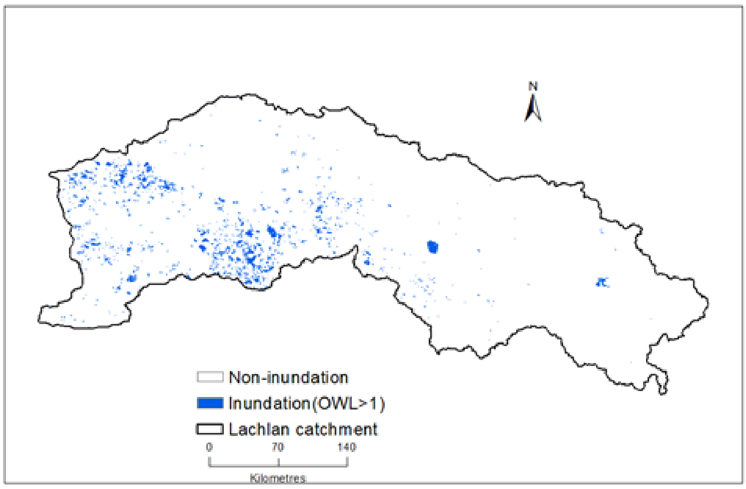
Figure S3

Example of weekly OWL inundation maps. (a) For week 16 in 2000: day 106-112; April 15-21), (b) after applying a threshold value of OWL > 1, (c) after applying a threshold value of OWL ≥ 10.

a)



b)



c)

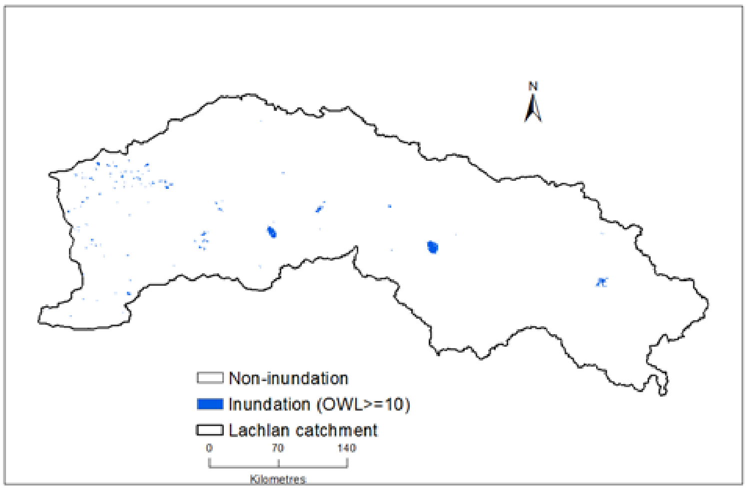
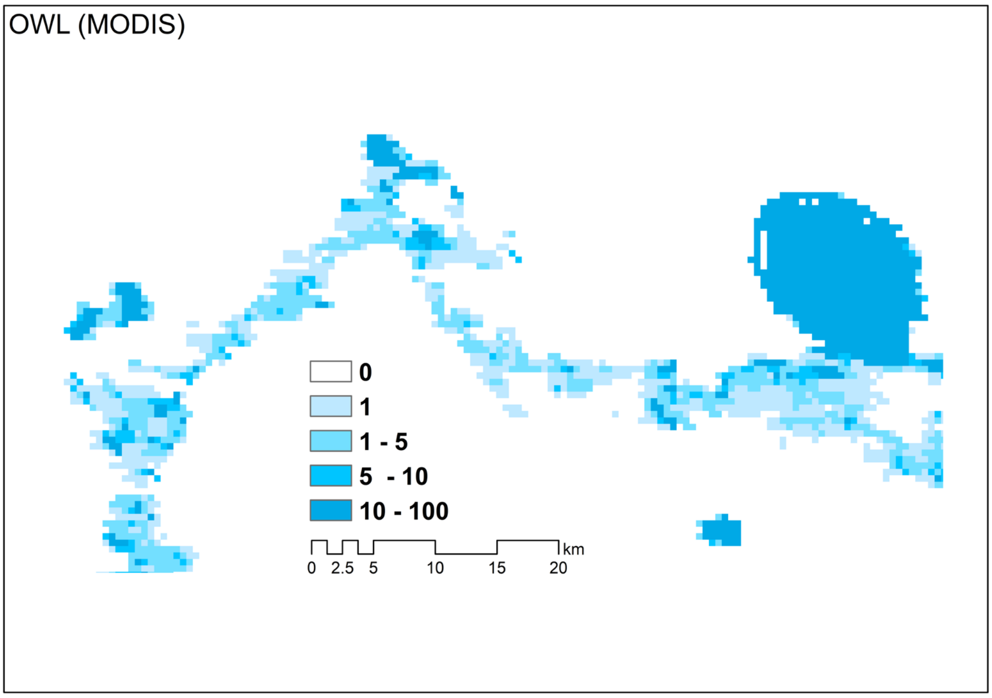


Figure S4

Inundation extent for week 50, Dec 10-16, 2000, representing daily flow of 51.224 GL. Top: RiM-FIM image (25 m resolution) is a weekly mean of the 3 RiM-FIM zones. Bottom: MODIS image (500 m resolution) shows an OWL value rang of 0-100 (no threshold applied).



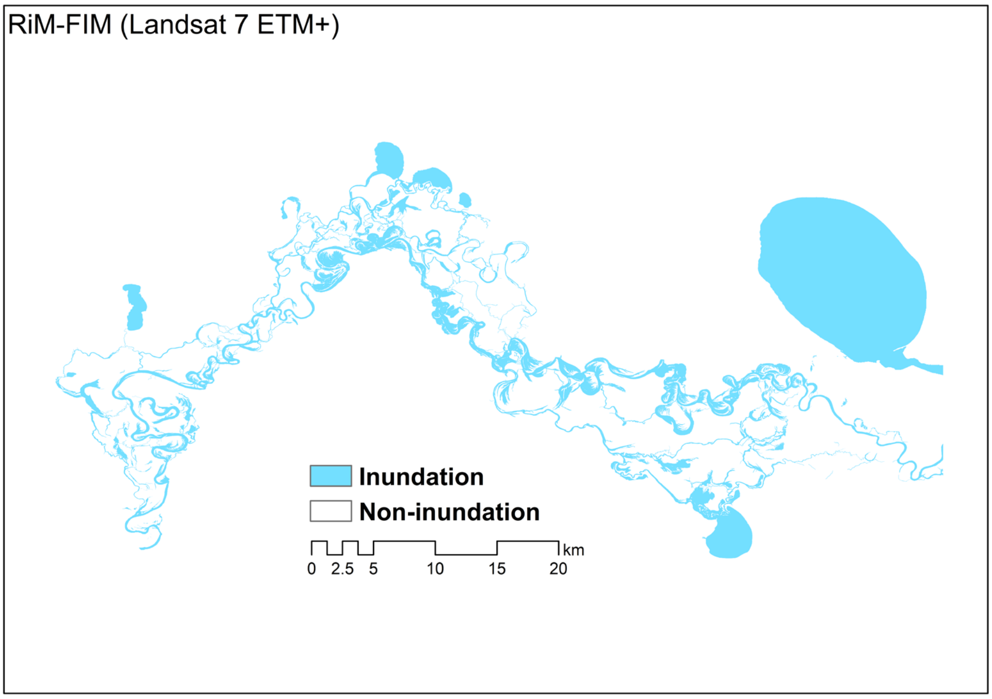
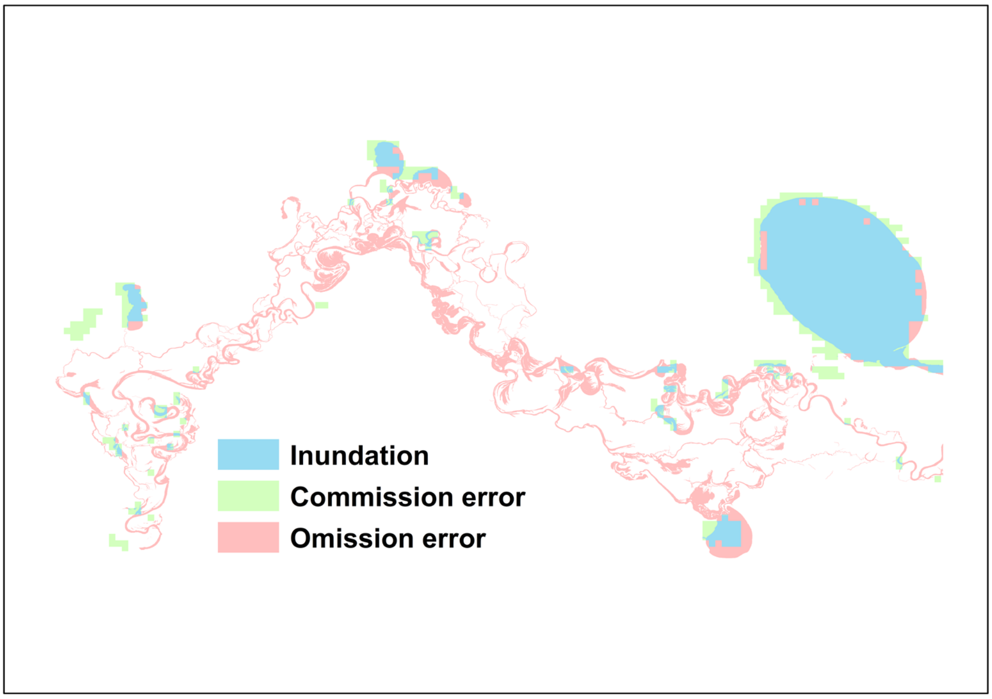


Figure S5

Results of MODIS vs. RiM-FIM comparison (top: OWL>1; bottom: OWL≥10). Commission error (over-estimation): RiM-FIM=non-inundation, OWL=inundation; Omission error (under-estimation): RiM-FIM=inundation, OWL=non-inundation



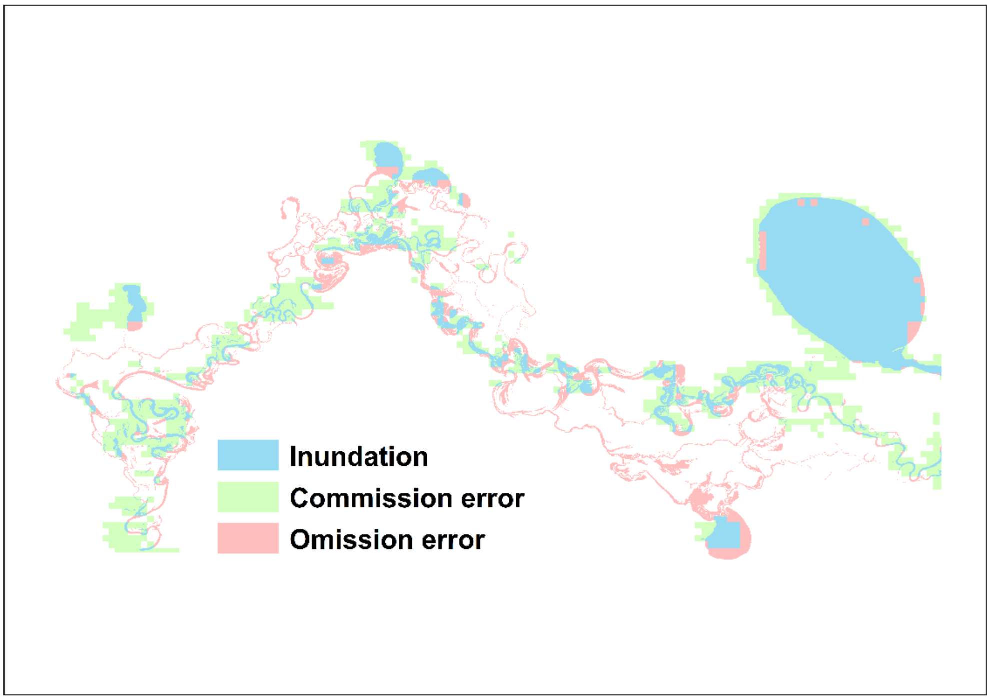


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Figure S6

Observed and simulated stream temperatures using different model parameterizations and flow rate for station 412194 (Lachlan River at 4 Mile). Observations (black lines), simulations (coloured lines), air temperature (grey lines). In 2009/10 during drought conditions no flow conditions prevailed generating false simulations for model parameterizations 4 and 8

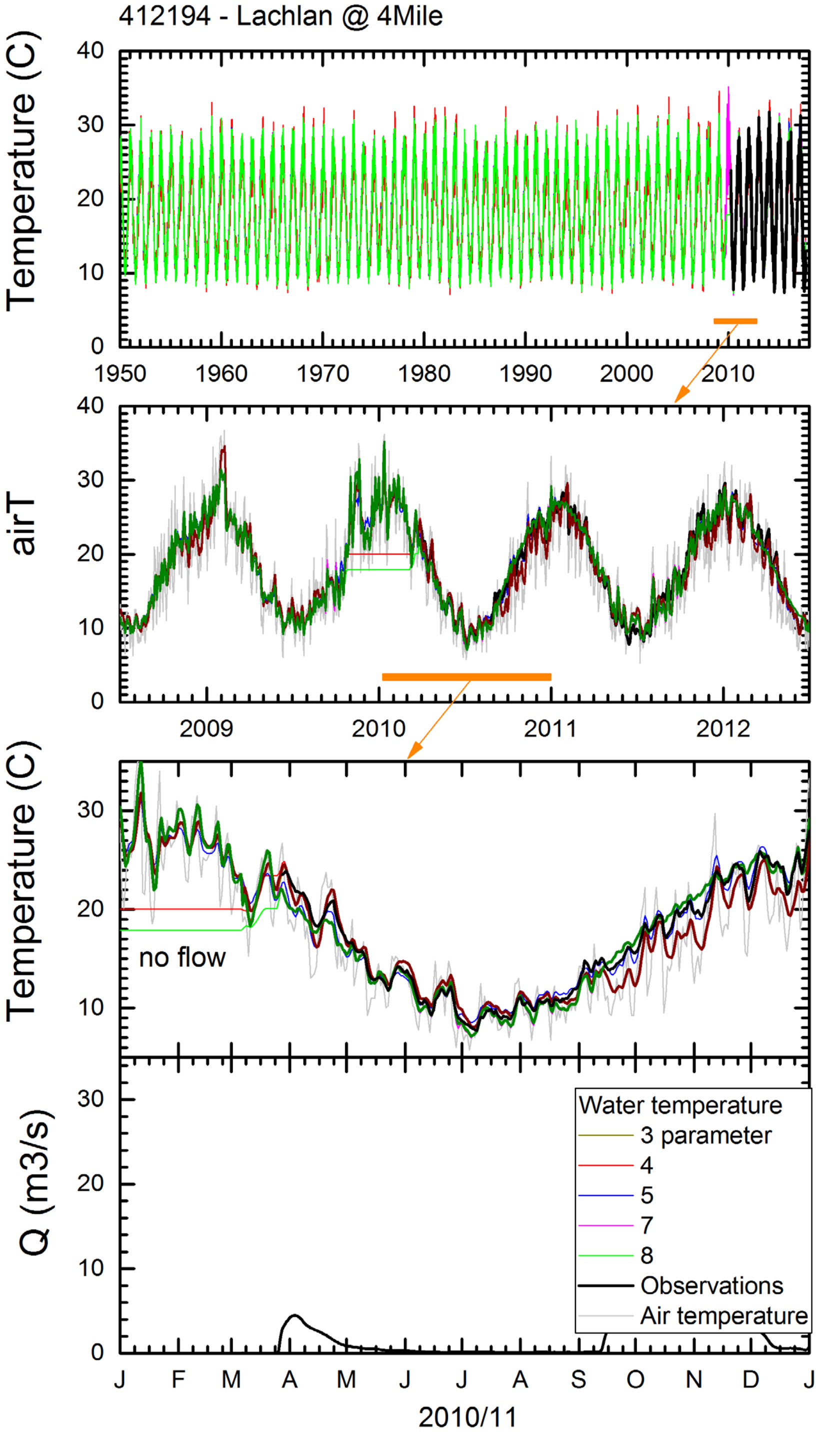


Figure S7

Hypsometric information for waterholes along the Moonie River (J. Marshall pers. comm.).

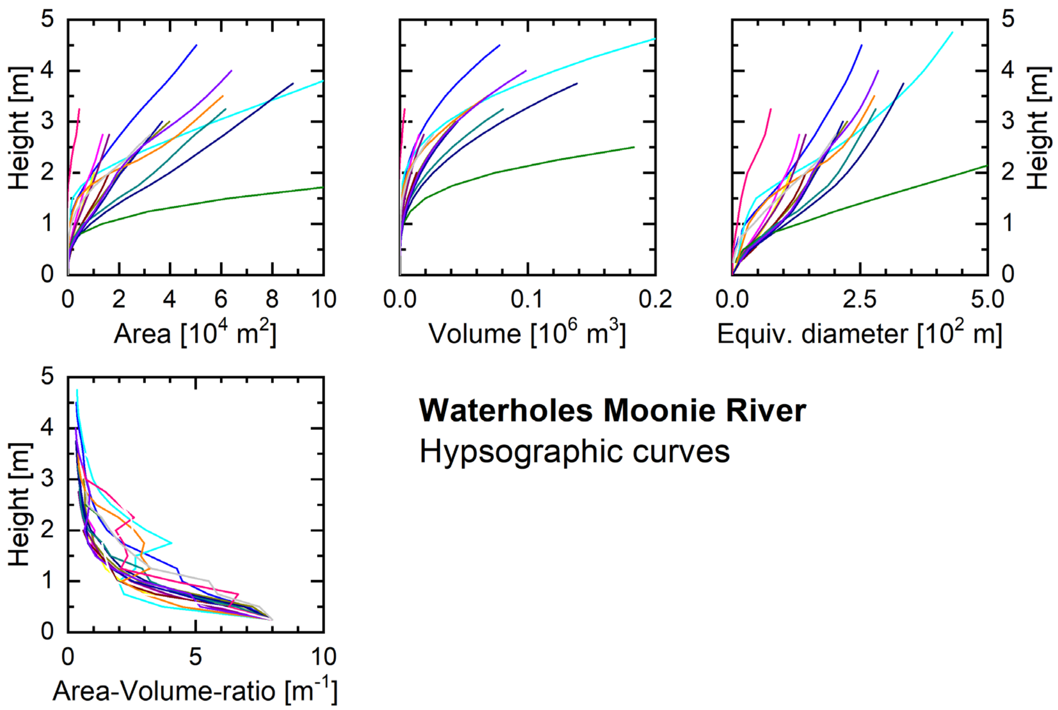
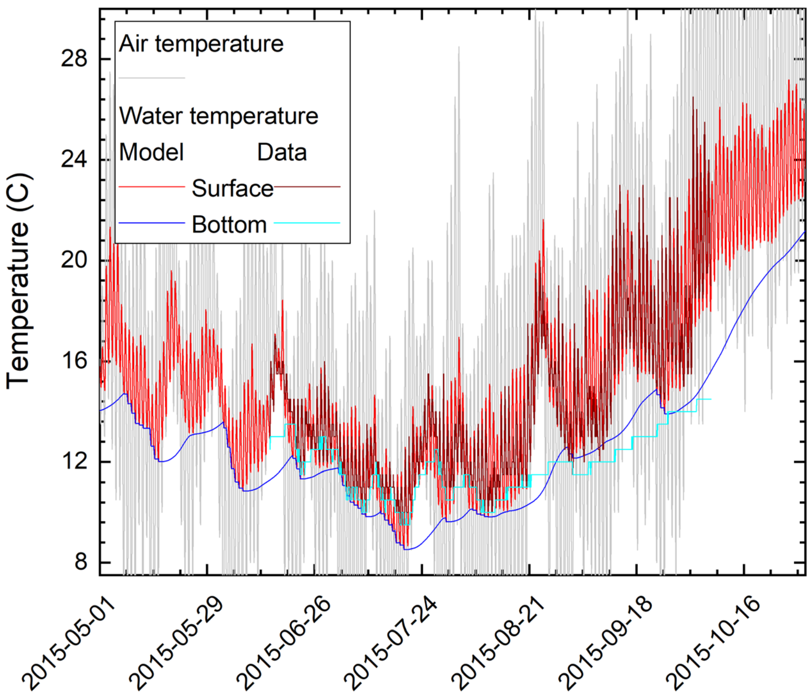


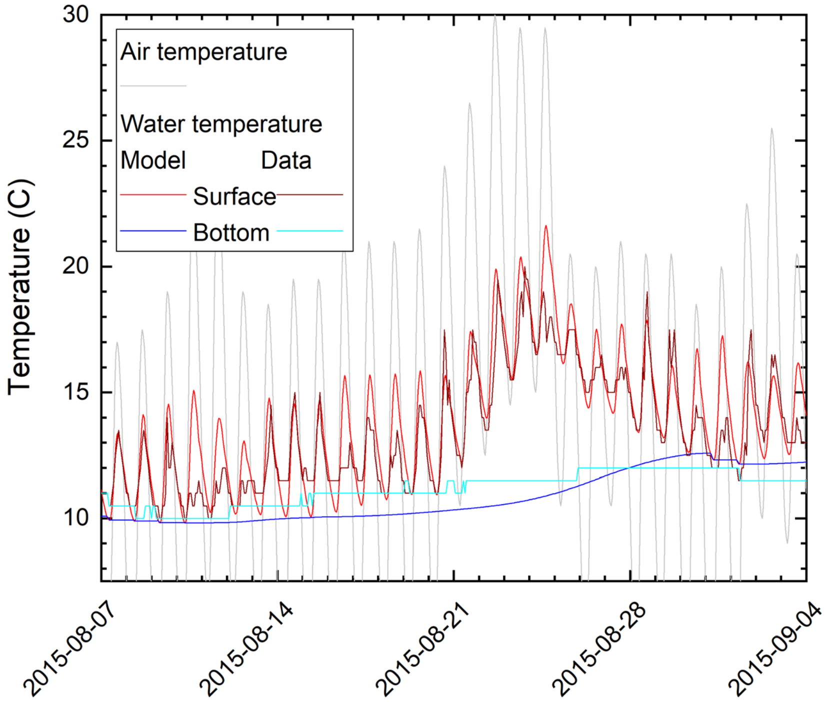
Figure S8

Simulated water temperature compared to measurements for the Brenda waterhole. a) Five month period containing measurements, b) zoomed in for a stratifying event.

a)



b)

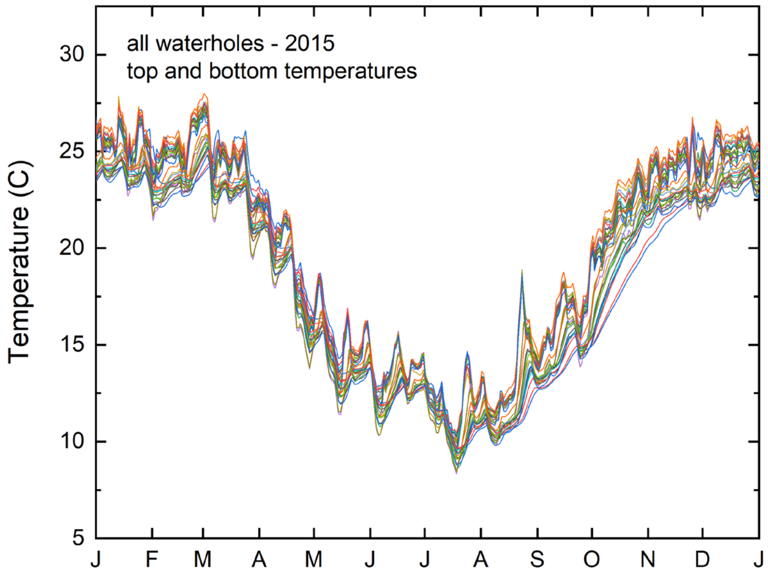


Air temperature
Water temperature
Model
Data
Surface
Bottom
Temperature (C)
30
25
20
15
10
2015-08-07
2015-08-14
2015-08-21
2015-08-28
2015-09-04

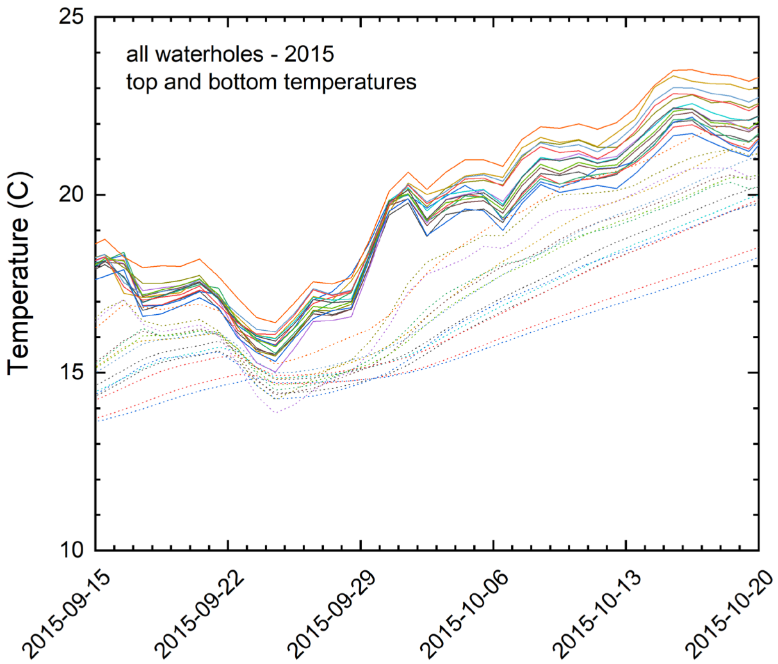
Figure S9

Simulated surface and bottom water temperatures for 15 waterholes in the Moonie River catchment, a) One year period, b) zoomed for a stratifying event.

a)



b)



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SECTION 2: Habitat Suitability Modelling

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Abstract

Common carp (*Cyprinus carpio*) are an invasive species of the rivers and waterways of south-eastern Australia, implicated in the serious decline of many native fish species. Over the past 50 years a variety of control options have been explored, all of which to date have proved either ineffective or cost prohibitive. Most recently the use of Cyprinid herpesvirus 3 (CyHV-3), has been proposed as a bio-control agent, but to assess the risks and benefits of this, as well as to develop a strategy for the release of the virus, requires a quantification of underlying process driving carp distribution and abundance. To this end we developed a novel process-based modelling framework which integrates expert opinion with spatio-temporal datasets via the construction of a Bayesian Belief Network. The resulting network thus enabled a prediction of the habitat suitability for carp across a range of hydrological habitats in south-eastern Australia, covering five diverse catchment areas encompassing in total a drainage area of 132,129 km^2 over a period of 17-27 years. This showed that while suitability for adults and sub-adult carp was medium-high across most habitats throughout the period, most habitats were poorly suited for the recruitment of larvae and young-of-the-year (YOY) for most years. Instead high population abundance was confirmed to depend on a small number of recruitment hotspots which occur in years of favourable inundation. Quantification of the underlying ecological drivers of carp abundance thus makes possible detailed planning by focusing on critical weaknesses in the population biology of carp. More specifically, it permits the rational planning for population reduction using the biocontrol agent, CyHV-3, targeting areas where the total population density is above a “damage threshold” of approximately 100 kg/ha.

Keywords

Biocontrol, common carp, Cyprinid herpesvirus 3, habitat suitability, hydrology, Murray-Darling basin

Introduction

Common carp (*Cyprinus carpio*) - hereafter referred to as carp - are recognised as the most serious invasive animal species of the waterways of south-eastern Australia (Koehn, 2004). Although there were several attempts at introductions of the fish in the nineteenth century, these were not particularly successful, and into the mid twentieth century the species had a restricted range within New South Wales (Shearer and Mulley, 1978). This situation changed drastically in the early 1960's as a result of a deliberate importation and dissemination of a European aquaculture strain ("Boolarra") into the Gippsland region of south-eastern Victoria (Wharton, 1971)). Once the authorities became aware of this introduction, an eradication campaign was attempted, but mainly due to the lack of effective control measures asides from poisoning infested waters, this campaign proved ineffective. Subsequently, carp underwent a rapid range expansion in the 1970's, and by the 1990's, surveys demonstrated that in some of the southern waterways of the Murray-Darling Basin (MDB) carp comprised over 95% of the fish biomass (Gehrke et al., 1995).

The main reason that the Victorian authorities had refused the request to import carp into Gippsland was the experience from North America, which had established common carp to cause extensive damage to waterways and lakes, particularly in the north-east of the United States. Initially this consisted of anecdotal reports of damage (Cahn, 1929), but these were confirmed by field studies comparing the response of aquatic vegetation and biodiversity following carp removal (Anderson, 1950; Cahoon, 1953; Threinen and Helm, 1954). Much of this destruction has been subsequently shown to be due to the feeding habits of adults, as although they can ingest food directly in the water column, they possess a specialised capability to forage in the substrate by filtering through the gills sediment which is sucked into the mouth. This benthivorous feeding behaviour can uproot plants and re-suspend sediments, reducing water clarity and hence light available for submerged aquatic plants and visual feeding fish (Huser and Bartels, 2015).

Nevertheless, carp are not always destructive to their aquatic environment, and in many parts of Europe, where much lower carp densities are encountered than in North America or Australia, ecological damage is rare (Crivelli, 1983). This has led to the concept of a "damage threshold" density wherein carp populations below the threshold have minimal adverse ecological impact (Zambrano et al., 2001). Although this threshold has not been fixed, in part due to the complexity of defining and measuring ecological damage, most studies place this threshold at a biomass of between 50 to 250 kg/ha (Vilizzi et al., 2015).

Given the importance of population density as a measure of potential and actual environment damage, being able to identify habitat that is highly suitable and will support high population densities is essential for rational management of invasive carp. However, measuring carp populations across broad landscapes, such as the MDB, is difficult. In part this is due to the intrinsic challenges of undertaking robust large area surveys of freshwater fish populations across diverse and varying hydrological habitats (Harris and Gehrke, 1997). However, as challenging is the extreme variability of carp populations due to southeast Australia's complex hydrology arising from extreme droughts related to the El Nino –Southern Oscillation (ENSO) cycle (Leblanc et al., 2012). Thus, a particular location during a flooding period may support extremely high carp populations, whilst during drought, populations may be low or even absent (Brown et al., 2005). Furthermore, carp have a successful life strategy of being able to actively select for and anticipate favourable recruitment areas, which enables them to have recruitment surges which can rapidly replenish the population (Bajer and Sorensen, 2010; Bajer et al., 2009).

A proven method of developing rational invasive species management is the use of habitat suitability modelling (Jimenez-Valverde et al., 2011), and this has been used to show the potential distribution of the species in Australia (Koehn, 2004) and North America. (DeVaney et al., 2009). However, to date, there has not been any published reports of applying habitat suitability modelling to estimate carp abundance, let alone abundance over time. A recent development in habitat suitability modelling for complex species-environment interactions, where populations have not yet stabilised or else are highly variable – is the use of "process" based modelling, whereby rather than relying on observed patterns of population presence or absence, the underlying ecological drivers leading to these patterns is modelled (van Klinken et al., 2015). In the case of invasive vertebrate species in Australia, this method has been successfully applied to rabbits (Murray et al., 2014) and feral pigs (Froese et al., 2017), but not yet to freshwater species. Furthermore, this methodology has not been applied specifically to develop time-series of populations estimates, which we reasoned were essential to understand carp population dynamics given their potential to undergo rapid increases. Herein, we describe how we successfully implemented process-based habitat suitability modelling to enable the identification of hydrological reaches and waterways where carp density is likely to be above the ecological damage threshold. The motivator for this identification – and the data resulting from the modelling, is to assist in the planning for how best to use Cyprinid herpesvirus 3 (CyHV-3) which has been proposed as biocontrol agent for common carp in southeastern Australia (SECTION 1).

Methods

Study system

The study system is described in SECTION 1. In brief, it consists of 5 catchments in southeastern Australia, four of which are within the MDB (the Moonie, Lachlan, mid Murray and lower Murray catchments) and one (the Glenelg) is a coastal River within Victoria (Figure 1). Each of these catchments have some unique features, such as the Moonie having summer rainfall, and a propensity for the main channel to dry in the winter, with waterholes acting as refugia for aquatic life (Marshall et al., 2016). The Lachlan covers a large expanse of central New South Wales (NSW), with upland fast flowing rivers in the east and slow flowing, highly regulated rivers in its western part (Hillman et al., 2003). The mid Murray encompasses a major wetland ecosystem, the Barmah-Millewa which is a known carp recruitment hotspot (Brown et al., 2005). The lower Murray is distinguished by being dry-land river flowing through a predominantly semi-arid environment with a low gradient, with frequent overflows resulting in complex patterns of wetland inundation (Robinson et al., 2015). The southernmost catchment, the Glenelg is, like the Moonie a low flow seasonal river, but by contrast is fed by winter rather than summer rainfall.

The temporal range for the habitat modelling also corresponded to that of the hydrological reconstruction and water temperature modelling described in SECTION 1. Initially the years between 2000 to 2016 were chosen in part due to the availability of MODIS imagery for estimating areas of inundation and the proposed time-step was monthly. After preliminary results were reviewed, the time-step was reduced to weekly and the temporal window expanded from 1990 to 2018. This enabled the modelling to review habitat dynamics due to La Niña and El Niño events, including the "Millennial Drought". However, for the Lachlan flow data for this earlier period was not available.

Bayesian Belief Network modelling

The process-based approach to habitat suitability modelling followed closely the methodology outlined by (van Klinken et al., 2015). (2015). In brief, the approach assumes that there are a restricted number of "key environmental variables" (KEV) which determine a species abundance, but which have a complex relationship, as they may interact with each other and the relationship between the KEV and the metric for abundance (usually a density measure) may be mediated by intermediate variables. Thus, for example, water temperature might be an identifiable variable for suitability, but this interacts with water velocity, which determines mixing, which in turns is influenced by slope. These complex interactions need to be resolved through the construction of a Bayesian Belief Network (BBN), a modelling approach now established in many domains involving a complex web of interactions and causation, including ecology and risk assessments (Milns et al., 2010).

Expert elicitation workshop

A facilitated workshop to elicit knowledge of the drivers of carp distribution and abundance and their interactions was held in October 2014 and was attended by 11 experts on carp biology and ecology. Following a review of existing published knowledge of factors influencing carp suitability, a consensus agreement was achieved on defining suitability rankings in terms of biomass density as being high (>100 kg live carp biomass /ha), medium (20-00 kg/ha) and low suitability habitat (<20 kg/ha).

Using entire group participation, experts then identified the KEVs associated with habitat suitability and how they were influenced by each other (Figure S1). This was followed by an exercise wherein the KEVs were more precisely defined, and then "discretised" into 2 or 3 categories with respect to their direct influence on carp suitability. Interactive effects of "parent" variables/nodes on "child" variables was handled by the experts dividing into small groups and assigning estimates of interactions in terms of resultant frequencies. A draft BBN model was then constructed and then presented to the experts for discussion.

Spatial data acquisition and initial Lachlan catchment BBN

The BBN model developed in the workshop was initially developed for the Lachlan on account of this catchment having a diversity of habitats and being relatively well studied with respect to carp ecology (Brown and Gilligan, 2014; Gilligan et al., 2010). Spatial layers were sourced for each of the "parent" nodes of the BBN corresponding to the KEVs (Table S1). For datasets that were time-invariant such as location, sediment type, waterway productivity or slope, the median value of the segment was taken. All time-series datasets were fragmented, missing or of sub-standard quality for specific time periods. To overcome these problems, and the need for surrogate data (where the KEV was not able to be sourced), we applied the following data modifications:

- Downstream flow. Where the river segment had a river gauge and there was an available reading then this value was enforced within the model otherwise the flow was modelled (SECTION 1)
- Inundation Modelling, where inundation was recorded within the satellite imagery this extent was allocated to the waterbody entity, refer to SECTION 1 for further details.
- Water temperature, was modelled as described in SECTION 1 for the reaches and several water storage locations. Where smaller waterbodies existed and were not implicitly modelled the nearest neighbouring reaches water temperature was allocated to the waterbody.
- Dissolved oxygen. This metric is not consistently recorded across all river gauges. Each case-study location was assessed on its own and values of appropriate states were assigned. (Table S1)
- Salinity. Electrical conductivity was used as a surrogate, as this is recorded by many (but not all) river gauges. The data that was available was used for the appropriate network unit and the recorded month. Where no data was available the habitat suitability state of "Good" was assigned based on the fact that within the Lachlan 99.34% of valid readings were defined in a state of "Good". This was also the case with the lower-Murray, mid-Murray and Moonie studies. However, the Glenelg was noticeably different with only 2 of the upper river gauges having a median habitat suitability classification of "Good" whilst the other 10 river gauges had a median state of "Moderate".

- Zooplankton. Minimal survey and no modelled data were available for the case study locations covering the temporal study window. To overcome this, we assumed that water body classification type (Table S2) and the water temperature was closely associated to zooplankton quantity.

All the KEV spatial layers were managed using a *PostgreSQL* database (v.10.10) using the *PostGIS* extension (v. 2.4.3). Each KEV dataset was allocated suitability states based on a set of predefined values for both larvae/YOY (Table S3) and sub-adults/adults (Table S4) An overall *PostgreSQL* database table was created from multiple materialized data views and exported to a comma separated vale (csv) file for each week within the case study. These files contained unique identifiers enabling the BBN to compute child node "beliefs".

A BBN was then constructed using *Netica* v5.24 with each node being populated with deterministic states or probability values based on results obtained through the expert elicitation workshop. *Netica* was then run directly from within *Jupyter Notebook* (*Python 2.7*) using the *Netica C API* (version 5.04 - Norsys Software Corp)). Bespoke *Python* code ran the model against the previously outputted weekly csv files creating the node beliefs for the *Netica* network file. The derived node beliefs were then written to a text file and imported back into the same *PostgreSQL* database used for the spatial data storage. Within the database the results were then merged with the spatial hydrological entities enabling summary maps of habitat suitability to be produced, using *Python 3.7, Geopandas 0.4.1 and CartoPy 0.17.0*.

For both the KEVs and the BBN outputs, the fundamental spatial unit was the hydrological reach (for rivers) and the waterbody (for inundation areas, reservoirs and lakes). These reaches/waterbodies were defined to have presumed uniform hydrological and ecological properties, and generally were delineated by combining several spatially defined segments using the algorithm defined in SECTION 1 ("Standardised methodology for delineation of reaches"). As the number of reaches/waterbodies was large, particularly for the Lachlan, the mid-Murray and the lower-Murray, we defined an aggregated unit – the hydrological zone – which were characterised by permanent barriers to connectivity, such as a dam wall. The number of zones varied from 4 in the Glenelg to 11 in the mid Murray. Zones within the Moonie followed that of the (DES, 2019) report, although zones 1 and 2 were both divided into 2 sub-zones at converging rivers to reduce the overall zone size. Zones established within (Brown and Gilligan;2014) where allocated to BBN entities within the Lachlan, Zone 8 was also included to represent Willandra Creek region. The Lower Murray zones were taken from the RIM-FIM zones, although renumbered from 1 below Lock 1 up to 10 which occurs between Lock 9 and Lock 10. The Mid-Murray region also aligned with the RIM-FIM zones and then included separate zones for the Campaspe and Goulburn Rivers. The Glenelg catchment was divided into 4 zones which represented the main Glenelg River and Wannon River.

Model refinement and extension to the other four catchments

Following on from the implementation of the BBN for the Lachlan catchment, the output was analysed, and consultations undertaken with domain experts in an iterative fashion. This resulted in various modifications as the understanding of the modelled system improved (Figure 2.3), the most important being:

- The single adult and juvenile suitability BBN were split into two separate BBNs as it became apparent that some of the KEVs for the two life stages were sufficiently distinct that they could not be subsumed into one BBN. This applied especially to the main environmental attributes driving juvenile recruitment, particularly waterway connectivity allowing the adults to move to the wetlands for spawning, which only affects juvenile population suitability.

- The need to explicitly identify, within the BBN, wetlands being in a state of flooding, as larvae (< 6 weeks) and young-of year (6 weeks to 1 year) were assumed to be predominately located there, whilst the sub-adults (> 1yr) and adults can be located within either the main channel or the wetland.
- Differentiating between larvae/YOY habitat suitability against the presence of larvae/YOY population suitability and the importance of adult carp accessing the highly suitable areas for spawning.
- The upper limit for the density estimate for highly suitable population state was shifted upwards from the 100 kg/ha estimated during the carp expert workshop to 200 kg / ha (~128 adult individuals) as this higher value had been measured by (Brown et al., 2005) in their study of the population biology of carp in the Murray valley, and it was assumed that similar high population densities could occur in the other catchments.
- The time step for the modelling was reduced from monthly to weekly as there existed too much variability within the flows and inundation.

During the model refinement the importance of adult connectivity to suitable wetlands become an apparent key to population suitability. Whilst the habitat may be a highly suitable location for larvae/YOY, if adult carp are prevented from accessing these locations then spawning cannot occur. To overcome this issue, we implemented a KEV of "adult connectivity". In creating this data, we looked at the potential for carp to move from reach to reach or reach to water-body. The NSW Barrier Impact dataset provided a ranking of impact to fish passage at various flow regimes and barrier types. For the Lachlan we could use this data directly, for the other case-study locations a visual assessment via *QIS 2.14* Bing Maps Aerial Imagery web map service was undertaken, reviewing barrier type. Where heights of barrier were known this was also used to derive an impact ranking.

This allocation then allowed for carp movements where percentile flows for each reach were associated to the barrier impact.

- Permanent impact of a barrier - whilst a small number of carp would travel downstream, no carp were allocated a movement upstream;
- Significant impact of a barrier to carp movements - a flow above the 95th percentile would allow carp movement in both directions;
- High impact of a barrier to carp movements - a flow above the 75th percentile would allow carp movement in both directions;
- Moderate-High or Moderate impact of a barrier to carp movements - a flow above the 50th percentile would allow carp movement in both directions;
- Moderate-Low or Low impact of a barrier to carp movements - a flow above the 25th percentile would allow carp movement in both directions;
- If a barrier was allocated a drown-out value, then this was applied to allocate both upstream/downstream movements when the hydrological flow was above this drown out value.

The BBN model was then extended to the other four catchments. Following consultation, the same thresholds for the KEVs were retained, but each catchment's hydrological modelling required modifications, based on the availability of source data (Table S1). As noted, the recognition that the temporal window used for the Lachlan River was dominated by the Millennial Drought led to the start date for the other four catchments being 1990. Asides from this, model construction, data management and output visualisation were the same for all other catchments as for the Lachlan River catchment.

Model evaluation

To assess the final BBN model, several workshops were held with domain experts for each of the studied catchments. The experts were shown the final BBN structure, and each of the primary spatial data layers for the KEVs was discussed, as to their appropriateness as a data source, as well as the assigned thresholds for levels corresponding to high, medium and low. The experts were then shown selective maps of the output - in terms of both the KEVs and the suitability output. For the latter, they were specifically asked to point out areas which did not agree with their personal experience and observations, and each of these "outliers" was discussed in detail as to reasons for disagreement. The feedback from each session was then incorporated into the next revision of the BBN, with the exception where expert recommendations were restricted to a single catchment and could not be generalised across the entire five case study catchments.

Biomass estimation and model validation

Conversion of suitability to biomass density (kg/ha) and population size

Biomass density estimates were defined during the expert elicitation workshop and classified against the three states. For 'High' a density of >100 kg/ha was allocated, where 'Moderate' was between >=20 and <= 100 kg/ha and 'Low' was < 20 kg/ha. After preliminary runs of the BBN, this range was further increased to 200 kg/ha (~80 adult individuals) as this higher value had been observed by Brown et al. (2005). We then associated downstream flow to habitat suitability and derived a simple lookup table (Table S5) which enabled a wider distribution of estimated kg/ha to various habitat states of reaches and waterbodies. Total live carp biomass for both sub-adults/adults and the larvae/YOY age class was then converted to a population size (i.e. number of individual fish) by assuming average weights of adults of 1.6 kg and for larvae/YOY 22g. These weights for the two age/stage groupings were derived from survey data within the Lachlan River Catchment which was extracted from the NSW Freshwater Fish Research Database (FFRD) on the 18th June 2013.

Habitat suitability model validation

For validation of our habitat suitability modelling, we used the total catchment biomass estimated by the NCCP Biomass Project (Stuart et al., 2019). This was provided in their Report's Table 9 (p. 46) biomass estimates – in total tonnes – for each of the 5 catchments, including 95% credible intervals. An additional ESRI shapefile was acquired from the Biomass Project which contained similar waterbody locations and rivers predicting biomass for each entity for week 20, 2011 across all case study locations. For rivers the density value was multiplied by the length and estimated width, whilst for waterbodies the area of shallow water in addition to the deep-water area was multiplied by the density to estimate overall biomass. We undertook a simple spatial intersection query to allocate zones to that of the habitat suitability so that a comparison of biomass could be undertaken at a catchment zone level.

Estimation of biomass density (kg/ha) in relation to damage thresholds

Whilst the area of waterbodies could be measured (SECTION 1), assignment of an area to the reaches was problematic. An average width had been assigned within the NCCP Biomass Project and therefore we assigned this width to the intersecting reach, but the allocation of a simple area calculation did not represent the area based on its weekly average flow. To overcome this, we calculated a 3-month moving average of rainfall over each catchment and then took the 20th and 80th percentile values over the entire temporal window. These percentiles where then used as cut-off values against the moving rainfall average. Where the monthly rainfall was below the 20th percentile then the average width was multiple by 0.6 representing a low flow state. When the monthly rainfall was within the percentile range the average width was used, whilst anything above the 80th percentile was allocated a width of 1.2 times the average width. Once the spatial unit has a density and an area allocated, we calculated the total biomass.

To assess impact, we adapted the concept of a "damage threshold", which hypotheses for invasive species there are threshold densities above which ecological damage occur (Norbury et al., 2015). For carp in south-eastern Australia, this has generally been considered to be ~100 kg/ha, but a recent comprehensive review of all published studies (Vilizzi et al., 2015) has proffered that varying thresholds exist for different impacts, with a much lower one for waterfowl and fish than for aquatic macrophytes and an even higher one for turbidity and nutrients. For our study we there apply three thresholds: at 50 kg/ha, 100 kg/ha and 150 kg/ha.

Results

Habitat Suitability for subadults/adults and larvae/YOY

Using the reconstruction of the key environmental variables as input into BBN, it was possible to obtain a weekly suitability classification for both sub-adult/adult and larvae/YOY populations for each reach or waterbody across the five catchments over the study period. Despite the enormous amount of resulting data (i.e. 18,179,344 habitat state classifications) clear patterns emerge when the data is summarised for each year for each catchment over the study period (Figure 2.4). For example, most of the catchments were of moderate to high suitability for sub-adults and adults throughout the period. An explanation of these patterns can be inferred from the BBN sensitivity analysis, which indicates the overwhelming importance of flow-related variables on classifying a river reach - where sub-adults/adults are preferentially found (Brown et al., 2005) - as being in a high suitability state (Figure 2.5). This is consistent with the analysis of the time series of the hydrological habitats, which shows that the river habitat was approximately constant in area for the four catchments over the study period (Figure 2.4a).

The exception to this favourable habitat state for sub-adults/adults was the Moonie in which a high proportion of the reaches/waterbodies were consistently classified to be in a low state throughout the study period (33.20%). This low state appears to be driven by the low agricultural productivity of catchment, which is dominated by grazing and dryland cropping with only a small area of irrigated agriculture for cotton and pasture (DES, 2018). Thus, fertiliser usage across the catchment is minimal, with resultant presumed low river and wetland primary productivity.

The processes and patterns for the suitability state for the larvae/YOY were more complex than for the adults/subadults. More specifically, high suitability required not only the habitat needing to be in a favourable state, but also the presence of spawning adults (Figure 2.3b), which for waterbodies off the main channel required enough flow to establish connectivity. This, and the intermittent flooding of many waterbodies, meant that there was more variation between catchments and zones within catchments (Figure S2). At one extreme was the Glenelg where all zones were in a low suitability state throughout the period (Figure S2a). Similarly, the Moonie was generally of low suitability except for one zone (Zone 5) which included 7 major waterholes (Appletree, Broadwater, Bullamon Plains, Kurrajong, Nullera, Nindigully Pub, and Nindigully) having an extended period of moderate suitability for larvae/YOY (23.13%) over the time-period (Figure S2e). In the other three catchments, the suitability pattern was more complex, as although many zones were mostly of low suitability, some - predominantly water-bodies - were of consistently in a moderate suitability state. Thus, in the Lower Murray, two large waterbody areas (Lake Bonney and Lake Victoria in Zones 4 and 8 respectively) could be considered recruitment "hotspots". In the Mid Murray, although there was no zone which was consistently in a high or moderate suitability state for larvae/YOY throughout the entire period comparable to the water-bodies in the Lower Murray, the Barmah-Millewa Forest (Zone 2) had periods of moderate suitability (corresponding to high flows) and in the adjoining Edwards River (Zone 11), the wetlands were generally in a state of moderate suitability for the larvae/YOY (Figure S2d). In the Lachlan, Lake Brewster and Lake Cowal (Zones 6 and 7 respectively) appears to serve as a recruitment hotspot in periods when they are flooded, while Lake Cargelligo (Zone 3) has more consistent suitability for spawning, albeit with a lower area than the other two lakes (Figure S2b).

Biomass density and population estimates for subadults/adults and larvae/YOY

Applying our conversion factor to the habitat state and the downstream flow (Table S5) allowed us to make an estimate of the total carp biomass for each reach/waterbody for each week, and when aggregated up, allowed us to estimate the total average biomass (in tonnes) at both a catchment ((Figure 2.6) and a zone level (Figure S2). There was considerable variation in the total biomass between the catchments (Table 1), with the lowest being the Moonie (73 tonnes) and the highest being the Lower Murray (3,493 tonnes). In general, this variation in total biomass was due to the number of subadult/adults, as although the YOY/larvae reached very large population sizes, their contribution to the biomass was only 12-17% of the total.

Although we calculated total biomass in each catchment and zone primarily to undertake the validation exercise (see below), the plots of the time trends are in general agreement with field observations of the population biology of carp. In particular, whilst the size of the population of subadults/adults is approximately constant over time, the population of larvae/YOY is highly dynamic, responding to favourable environmental conditions to allow periodic massive recruitment events. This can be seen in the case of Zone 2 in the Mid-Murray (the Barmah-Millewa Forest) where our modelling indicates a spike in recruitment in 2000 in response to the flooding of the wetlands (Appendix 1.14), which agrees with the observations made in a detailed carp population biology study by Brown et al. (2005).

Model validation

Applying a comparison of these estimates for the 32 hydrological zones for week 20 of 2011 with those supplied by the NCCP Biomass Project showed a poor agreement, with a correlation co-efficient (r) of only 0.11 (Figure 2.7a). A close inspection of data of the two extreme outlier points showed these to be intermittently flooded water-bodies in the Lachlan and the Mid-Murray, we hypothesised that as the Biomass Project had used for their estimates the spatial area delineated in the Australian National Aquatic Ecosystem dataset, which is the maximum area, this might account for the large difference. This was confirmed by undertaking a mapping exercise, which showed that for both waterbodies in May 2011, the actual inundated area - which we estimated by either satellite imagery or RiM-FIM inundation modelling - was considerably less than the area of the spatial object (Figure S3). We therefore adjusted the Biomass Project estimates to consider the actual areas of inundation and reran the comparison, which demonstrated a very high correlation $r = 0.92$ (Figure 2.7b).

Density estimates in relation to ecological damage

The calculation of the carp density (kg/ha) in relation to the ecological damage thresholds for carp allows a catchment area estimation of how the impacts of carp compare over time and between catchments. Taking the 100 kg/ha limit, one can see that in the Glenelg, the median carp density is mostly below that for damage to aquatic macrophytes (i.e. 100 kg/ha) but above that for detrimental impacts for native fish (i.e. 50 kg/ha) (Figure 2.8a). The low carp density in the Moonie suggests that overall damage there is even less, although the observation that carp can reach high densities in drying waterholes suggests the need for a zone-level analysis, and for Zone 5, which contains a large number of waterholes, the median density can reach 130 kg/ha (Figure S4). Where there is less ambivalence is the very high biomass densities estimated for the two Murray river catchments, which exceed the threshold of 150 kg/ha at which water turbidity effects occur. The Lachlan was intermediate in its overall density, being above the 100 kg/ha threshold, but below 150 kg/ha.

Discussion

As far as we are aware, this study represents the first attempt to reconstruct time-varying habitat process-based suitability over a wide geographical area and at high spatial resolution for a vertebrate species. Of these three characteristics – space, time and scale – it is unquestionably the implementation of time-varying habitat suitability that is most innovative. Already process-based modelling has been used at high spatial resolution to determine priority areas for conservation for an endangered marsupial (Smith et al. (2007), and Murray et al. (2014) developed a wide area BBN model to guide population control for invasive rabbits over an area of almost 300,000 km^2. However, both these models used only time-averaged spatial predictors. More recently, Froese et al. (2017) mapped habitat suitability for feral pigs in northern Australia over both the wet and dry season, and highlighted the considerable difference in suitability between the two seasons, and thus implicitly the dangers of ignoring the temporal element where the species has a critical dependence on a resource, in this case water. Our modelling is thus a logical extension to this approach, where instead of modelling two generalised seasons, we estimated habitat suitability for each reach and waterbody over an extended period (17-27 years). This allowed us to detect the obvious spatial trends within catchments (e.g. the poor suitability of the eastern upland part of the Lachlan catchment versus the more suitable western, lowland part) as well as those between catchments (e.g the poor suitability of the Glenelg and Moonie for the YOY/larvae versus the more favourable suitability of the lower Murray). Combined with the high-resolution time-step (i.e. weekly), we were able to pick up temporal trends, such as the pulsatile variability in the area of suitability in the mid Murray as compared to the more gradual changes in suitability in the Lachlan. Accepting that quantifying this variability is essential for understanding and modelling the population dynamics of carp, it is clear that if we had used an "averaged" habitat suitability model, the results would not have provided the insights that our high-resolution spatiotemporal modelling provided.

Of these insights, the most important undoubtedly was being able to define those catchments in which carp population are above the hypothesised damage threshold and need to be priority areas for control. This type of analysis has a wider context in invasive species ecology, as it is a specific instance of the "density impact" (or "density-damage") concept, *viz.* that the higher the density of an invasive species the greater will be its detrimental impact (Bomford and Tilzey, 1997). Whilst this concept has received considerable theoretical attention – and indeed has become somewhat of a unifying theme for managing invasive species (Yokomizo et al., 2009) – an ongoing challenge is to define this relationship for a particular invasive species and apply the concept in a practical manner (Norbury et al., 2015). In the specific case of carp, our modelling of time-varying habitat suitability has enabled us to make an estimate of biomass abundance density (in kg/ha) for each reach/waterbody, and combining this with the recent quantification of the damage threshold or carp damage, enabled us to confirm that catchments with relatively high flow with intermittently inundated wetlands – such as the mid and lower Murray – must be treated as priority catchments for control as density was shown to be consistently above the damage threshold for all the modelled years.

As importantly as being able to identify catchments for population control is the possibility to identify those areas where control may not be needed, as their densities are beneath the threshold. This is particularly relevant for the proposed use of CyHV-3 for population control, as arguments have been presented against the use of virus on account of the damage it might induce in hydrological ecosystems due to the death and decay of the fish (Kopf et al., 2019; Lighten and van Oosterhout, 2017; Marshall et al., 2018). This "carpageddon" argument assumes that the virus will be released in all catchments and the resulting large-scale and widespread scale mortality events will obviate any possibility of managing adverse consequences such as localised anoxia in low flow waterways. Extrapolating our findings from the study catchments to the rivers and waterways of south-eastern Australia, it is highly likely that in a large proportion, carp density is below the damage threshold and thus population control through release of the virus in these is not warranted, and thus risk of adverse impacts can be greatly reduced and/or managed.

The potential selective release of CyHV-3 does not of course depend on the epidemiological behaviour within carp population, and in particular whether it will be able to spread readily between catchments due to fish movements. Equally important is whether the population will be able to rebound rapidly following the initial knockdown due to development of resistance and/or the reproductive potential of surviving fish (Becker et al., 2019). However, these factors are all interwoven with the underlying ecology of the rivers and waterways, and as has been shown with our temperature modelling (SECTION 1), simplistic assumptions of how the virus will behave if released in Australia which do not take this complexity into account need to be treated cautiously (Boutier et al., 2019). This there is a strong argument that only by developing models which integrate ecology, demography and epidemiology is it possible to fully explore and predict how the virus might behave following a release into the complex system of the riverine ecology of south-eastern Australia (SECTION 3 and 4).

Conclusion

The adoption of a Big data-driven modelling approach has enabled us to reconstruct estimates of carp biomass and abundance over a wide spatial area of south-eastern Australia at a fine spatial scale and for most of the studied catchments, for a period extending over 25 years. This provides insight into the fundamental drivers of the invasiveness of the population, confirming field-observations and other modelling studies (Brown and Gilligan, 2014; Brown et al., 2005) that while the rivers are consistently highly suitable for sub-adult and adult growth and survival, they provide little suitable habitat for spawning, which preferentially occurs in waterbodies, and particularly in off-channel, periodically inundated floodplains. However more importantly from the perspective of developing strategies for the control of carp, this work now makes possible biologically realistic and transparent in-silico scenario modelling, in which the success (or otherwise) of control options, such as commercial harvesting or the use of a viral biocontrol agent, can be explored by counterfactually implementing these in the past and comparing the resulting alternative impact on populations as compared to the modelled estimation of reality. Nevertheless, the outputs from our modelling - abundance density for two age classes (subadults/ adults and larvae/young-of the-year) - are crudely derived from the weekly habitat suitability estimate and while we consider this is suitable for averaged annual estimates this may not be suitable for modelling at a fine temporal scale where rapid changes in suitability state will not equate to corresponding declines or increases in population. To enable we propose the need to develop a full demographic population model for carp, where each age class can be projected forward with the two demographic parameters - recruitment and survival - linked to and derived from our habitat suitability modelling output, which will be facilitated by the recent publication of a demographic model for carp for the Murray River (Koehn et al., 2017).

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Last and foremost, we thank the NCCP project team (Jamie Allnutt, Jennifer Marshall, Toby Piddocke and Matt Barwick) without whose support and encouragement this complex project would not have come to fruition.

Tables

Table 1

Summary statistics for habitat suitability, biomass and population size for the 5 catchments.

a. Glenelg River catchment

Grouping	Parameter	Median (50th) percentile	Lower 5th percentile	Upper 95th percentile
Habitat Classification (ha)	River	1,738	1,446.65	1,948.08
	River Wetland	0	0	0
	Lakes	2,597.36	319.38	6,138.08
	Wetland	0	0	0
	Floodplain	0	0	0
	No Water	26.12	2.31	208.05
Sub-Adult / Adult Habitat State (ha)	High	1,702.22	829.94	3,942.97
	Moderate	2,303.30	1,060.98	4,033.45
	Low	93.45	54.84	125.49
	Not Suitable	0	0	0
Larvae / YOY Habitat State (ha)	High	0	0	0
	Moderate	22.43	13.81	32.32
	Low	4,076.04	1,898.96	7,954.22
	Not Suitable	19.22	0	205.94
Estimated biomass (tonnes)	Sub-Adult / Adult	347.72	174.91	624.93
	Larvae / YOY Habitat	69.52	31.53	126.85

Estimated population (No.)	Sub-Adult / Adult	222,513.80	111,790.32	400,049.50
	Larvae / YOY Habitat	3,160,640.85	1,433,261.89	5,766,950.77

b. Lachlan River catchment

Grouping	Parameter	Median (50th) percentile	Lower 5th percentile	Upper 95th percentile
Habitat Classification (ha)	River	5,828.18	5,068.26	6614.96
	River Wetland	88.944	45.35	981.51
	Lakes	5,961.50	1,628.92	16,375.11
	Wetland	75.34	29.58	2475.70
	Floodplain	1,228.85	33.55	6630.65
	No Water	367.87	104.89	566.96
Sub-Adult / Adult Habitat State (ha)	High	8,370.70	5,273.36	12,291.29
	Moderate	5,909.72	1,975.14	19,908.02
	Low	17.30	6.90	25.31
	Not Suitable	367.87	104.90	566.96
Larvae / YOY Habitat State (ha)	High	0.55	0.00	1,497.65
	Moderate	2,461.12	389.43	15,161.50
	Low	10,611.47	6,882.75	15,315.38
	Not Suitable	367.87	104.90	566.96
Estimated biomass (tonnes)	Sub-Adult / Adult	1,524.97	751.66	3380.1

	Larvae / YOY Habitat	278.5	108.88	889.44
Estimated population (No.)	Sub-Adult / Adult	973,361.76	479,847.51	2,158,843.62
	Larvae / YOY Habitat	12,646,875.05	4,958,287.6	40,413,759.99

c. Mid Murray River catchment

Grouping	Parameter	Median (50th) percentile	Lower 5th percentile	Upper 95th percentile
Habitat Classification (ha)	River	4,275.09	2,597.62	4,943.32
	River Wetland	1,219.99	905.16	6,330.21
	Lakes	579.66	207.77	700.99
	Wetland	1,200.39	698.92	5,447.39
	Floodplain	237.38	188.11	282.53
	No Water	396.69	31.64	658.05
Sub-Adult / Adult Habitat State (ha)	High	5,515.57	4,706.31	8,183.39
	Moderate	2,435.34	1,546.44	9,234.26
	Low	0	0	0
	Not Suitable	0	0	0
Larvae / YOY Habitat State (ha)	High	63.31	43.05	83.25
	Moderate	1,825.55	1,400.88	9,132.29
	Low	5,634.77	4,316.73	8,059.51
	Not Suitable	396.69	31.64	658.05

Estimated biomass (tonnes)	Sub-Adult / Adult	1,157.26	919.4	2,706.93
	Larvae / YOY Habitat	251.94	186.33	704.91
Estimated population (No.)	Sub-Adult / Adult	739,983.57	587,765.22	1,731,946.68
	Larvae / YOY Habitat	11,417,985.19	8,445,976.12	31,998,230.16

d. Lower Murray River catchment

Grouping	Parameter	Median (50th) percentile	Lower 5th percentile	Upper 95th percentile
Habitat Classification (ha)	River	5,725.93	4,539.12	6,703.55
	River Wetland	7.30	3.06	14.10
	Lakes	14,862.79	9,846.92	16,702.45
	Wetland	3,018.22	1,026.26	5,010.16
	Floodplain	827.86	486.06	3,457.51
	No Water	46.01	0.78	74.01
Sub-Adult / Adult Habitat State (ha)	High	13,691.31	11,007.17	17,315.24
	Moderate	9,579.82	7,303.65	13,490.52
	Low	0	0	0
	Not Suitable	0	0	0
Larvae / YOY Habitat State (ha)	High	221.57	135.11	1,533.70
	Moderate	16,959.36	12,365.20	22,922.97
	Low	6,488.07	5,317.31	7,467.72

	Not Suitable	46.01	0.78	74.01
Estimated biomass (tonnes)	Sub-Adult / Adult	2,965.37	2,403.03	4,134.35
	Larvae / YOY Habitat	527.22	395.99	870.81
Estimated population (No.)	Sub-Adult / Adult	1,892,497.97	1,533,044.32	2,638,940.35
	Larvae / YOY Habitat	23,836,888.11	17,929,342.87	39,477,039.86

e. Moonie River catchment

Grouping	Parameter	Median (50th) percentile	Lower 5th percentile	Upper 95th percentile
Habitat Classification (ha)	River	440.09	213.37	661.38
	River Wetland	21.48	10.76	30.83
	Lakes	228.69	32.13	501.44
	Wetland	50.24	23.73	88.30
	Floodplain	0.67	0.00	1.36
	No Water	228.69	32.13	501.44
Sub-Adult / Adult Habitat State (ha)	High	348.52	157.32	608.94
	Moderate	340.70	226.79	450.27
	Low	316.74	266.69	355.77
	Not Suitable	8.44	1.93	21.07
Larvae / YOY Habitat State (ha)	High	0.03	0.00	0.15
	Moderate	170.69	48.23	434.96

	Low	543.46	337.81	764.35
	Not Suitable	240.46	111.64	411.23
Estimated biomass (tonnes)	Sub-Adult / Adult	63.79	36.58	91.65
	Larvae / YOY Habitat	9.27	3.78	16.01
Estimated population (No.)	Sub-Adult / Adult	40,725.81	23,309.44	58,545.78
	Larvae / YOY Habitat	422,034.48	172,783.49	725,428.34

Figures

Figure 2.1.

An overview map of the study showing the location of the study catchments in relation to the main rivers of the Murray-Darling Basin (MDB). For the five study catchments, seasonality plots are given for our estimates of the average discharge (ML/day) and average water temperature (°C) – see SECTION 1 for how these were calculated.

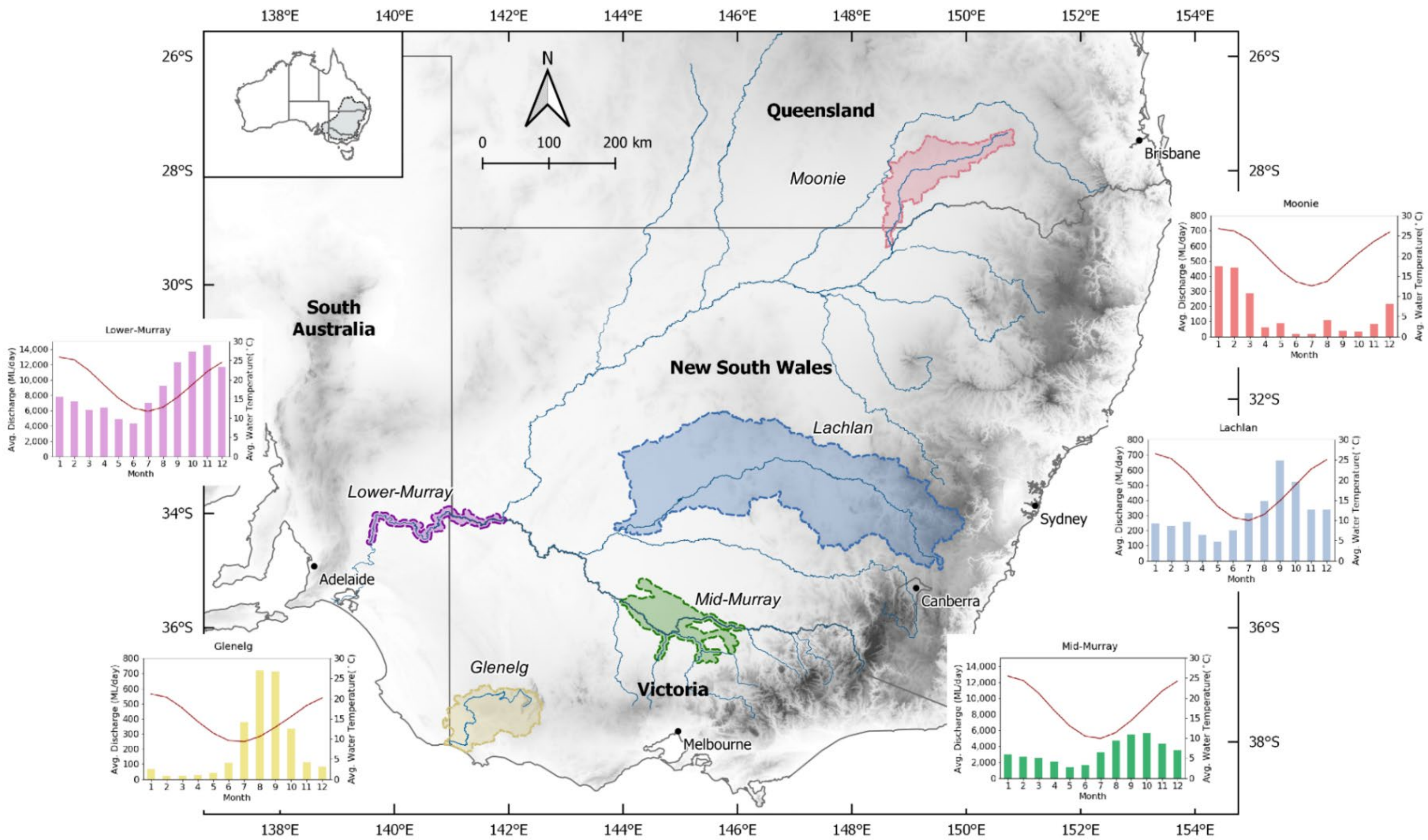


Figure 2.2

The workflow for developing the Bayesian Belief Networks (BBN) for adult/subadults and larvae/YOY, grouped into three general stages: Conceptual model development, the BBN model development and the BBN model deployment and validation. Adapted from Figure 2 in Smith et al. (2007)

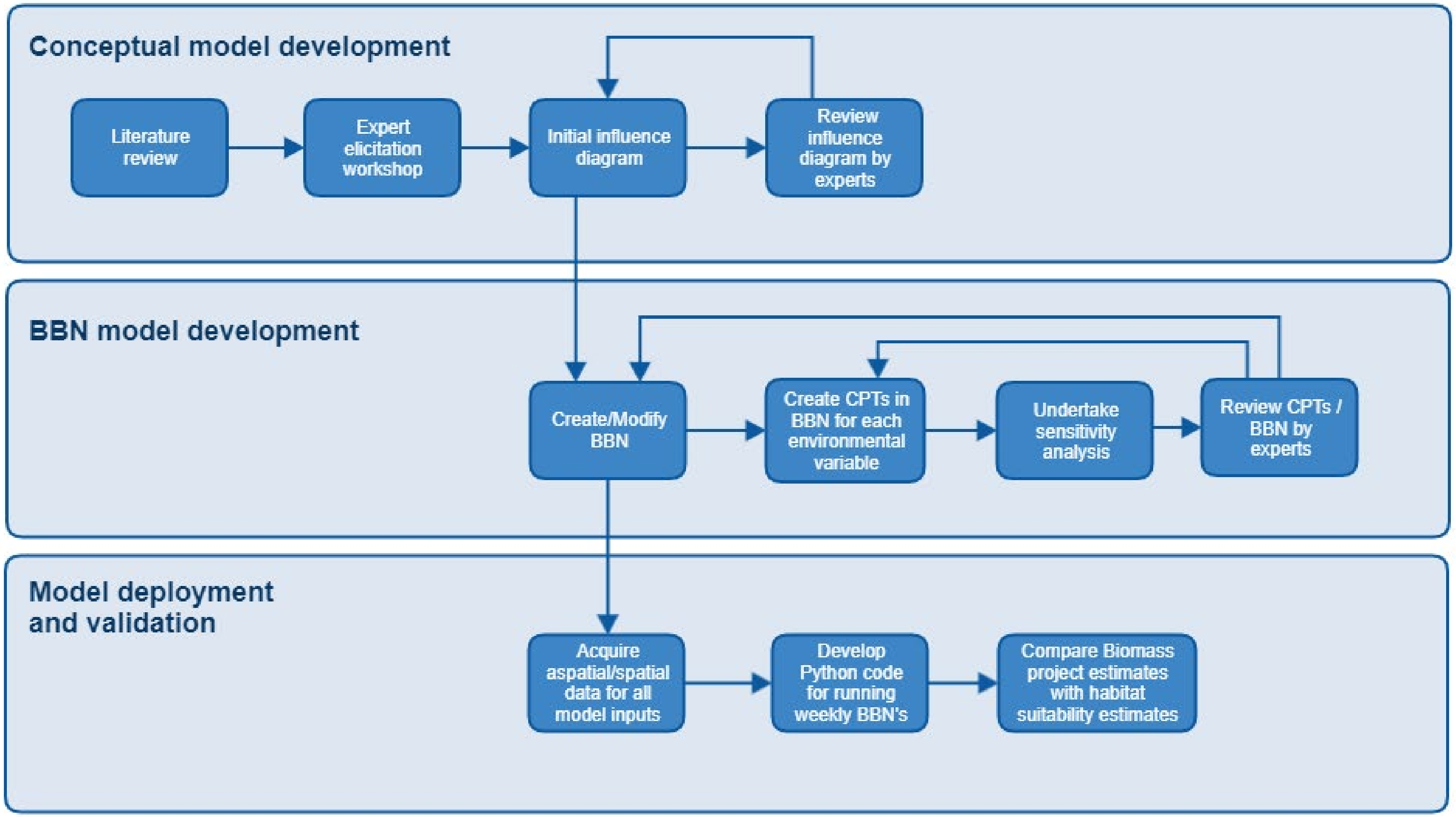
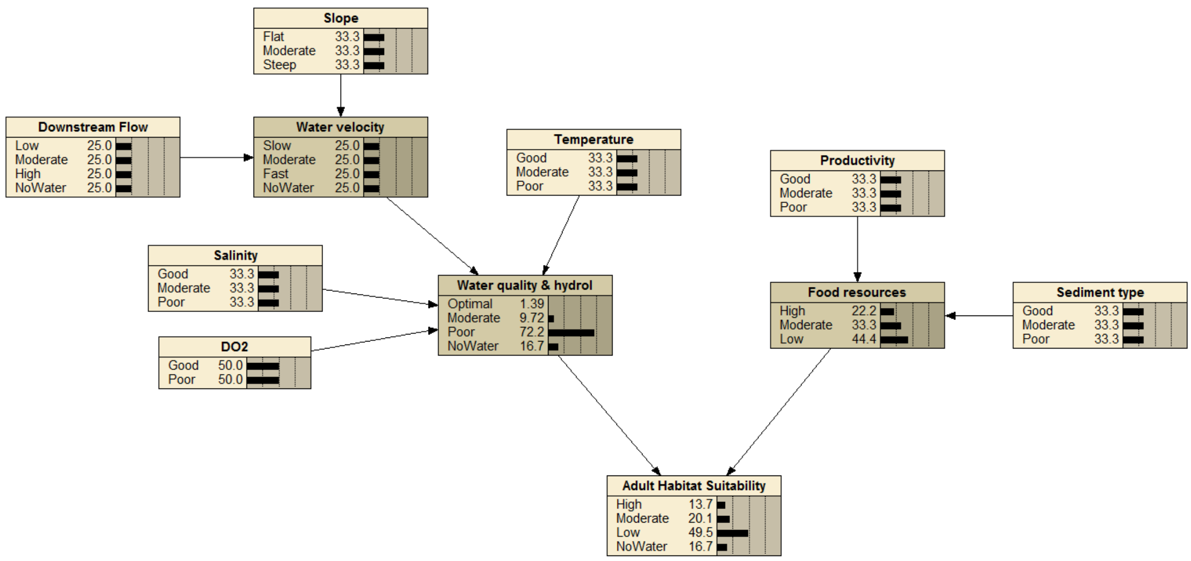


Figure 2.3.

The final Bayesian Belief Network (BBN) for carp habitat suitability in south-eastern Australia for (a) subadults/adults; and (b) larvae/young of year (YOY).

(a) Sub-adult and adult BBN



(b) Larvae and YOY BBN

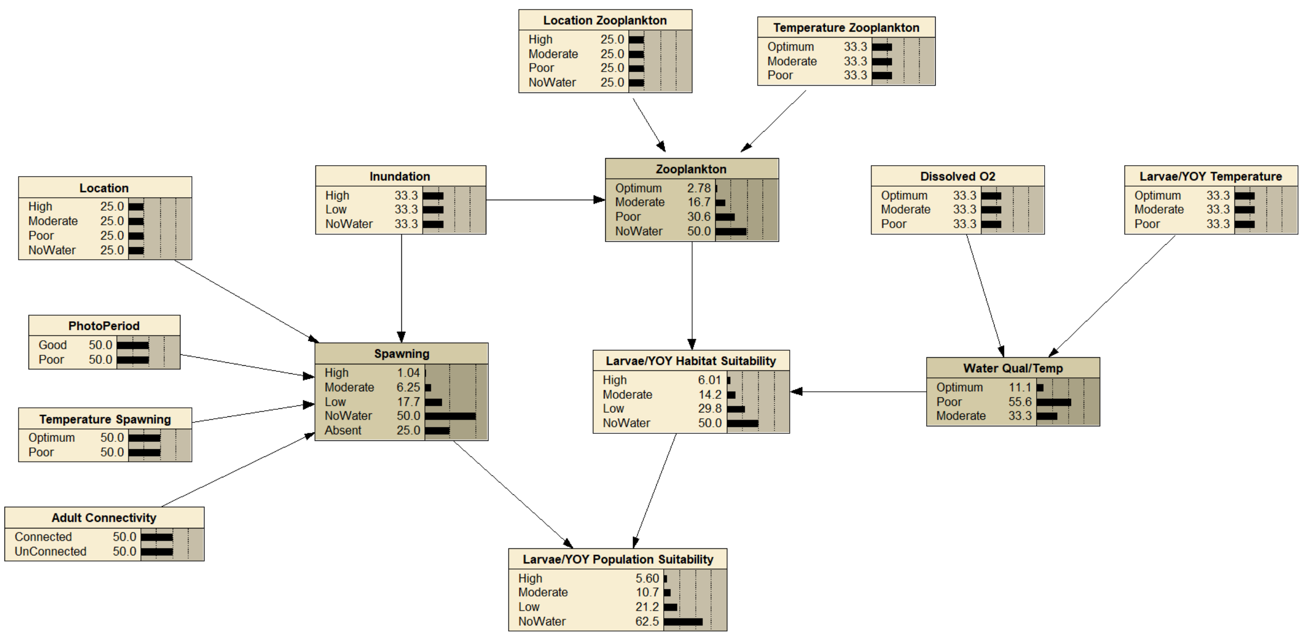
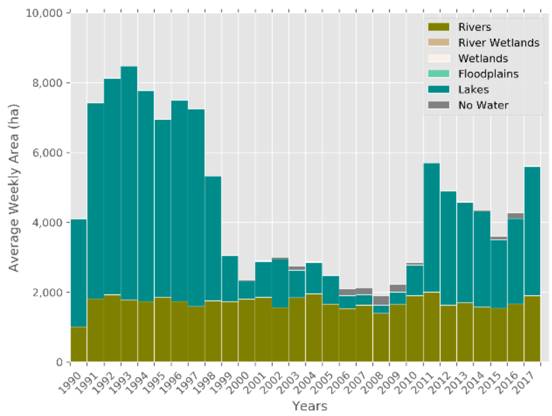


Figure 2.4.

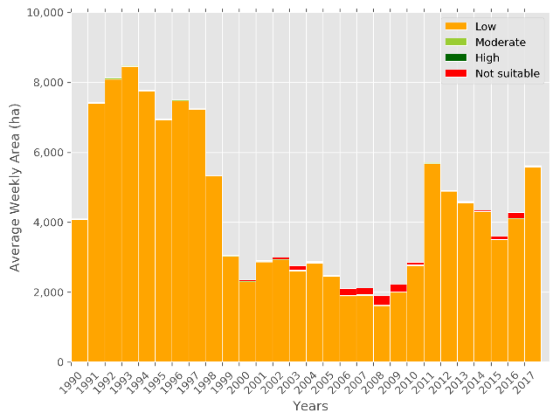
Time series stacked barcharts for each of the study catchments showing (a) the areas of the different hydrological classes; (b) the larvae/young-of-year habitat suitability; and (c) the sub-adult/adult habitat suitability state. Note that due to the variability in each case-study catchment, the y-axes have different maximum values.

Glenelg River catchment (y-scale max: 10,000 ha)

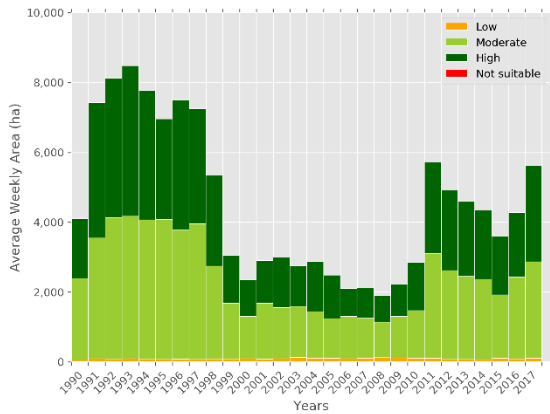
(a) Hydrological classes



(b) Larvae / YOY suitability

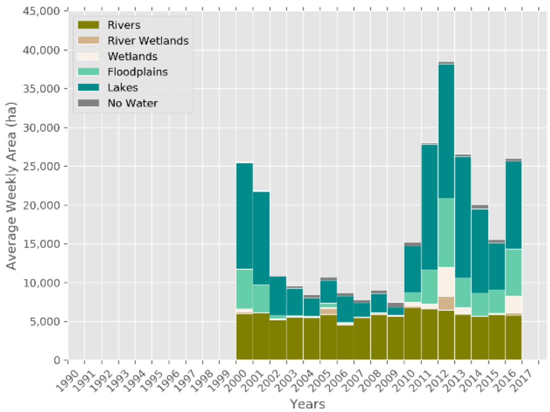


(c) Sub-adult / Adult suitability

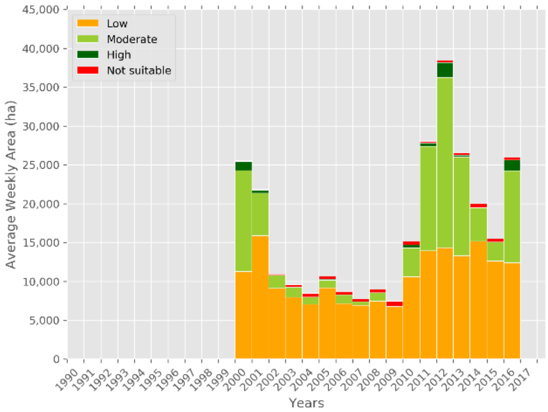


Lachlan River catchment (y-scale max 45,000 ha)

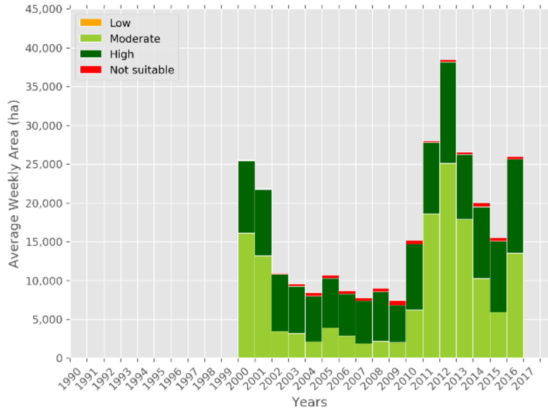
(a) Hydrological classes



(b) Larvae / YOY suitability

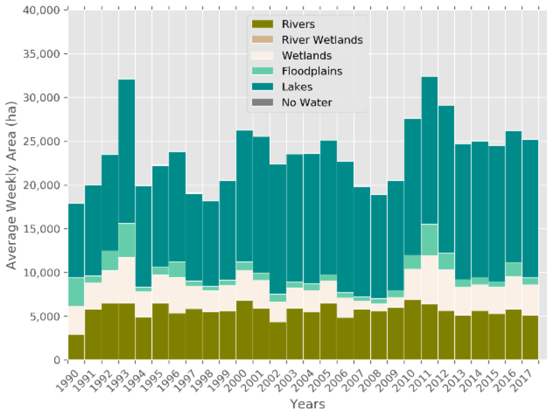


(c) Sub-adult / Adult suitability

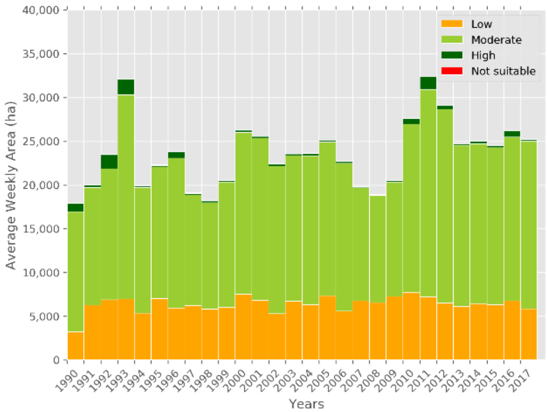


Lower Murray River catchment (y scale max: 40,000)

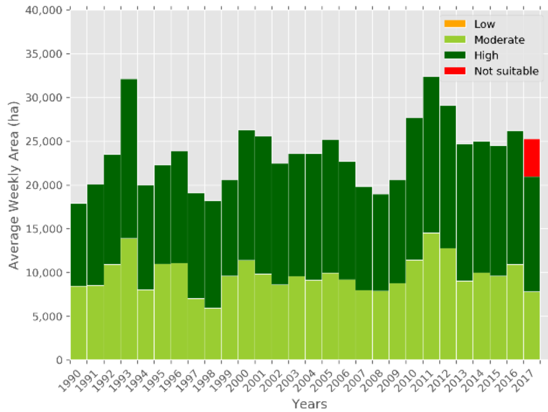
(a) Hydrological classes



(b) Larvae / YOY suitability

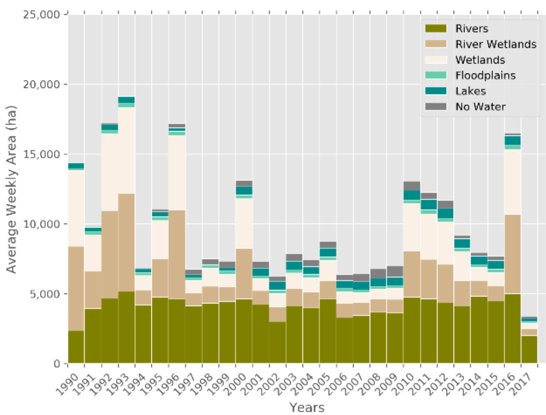


(c) Sub-adult / Adult suitability

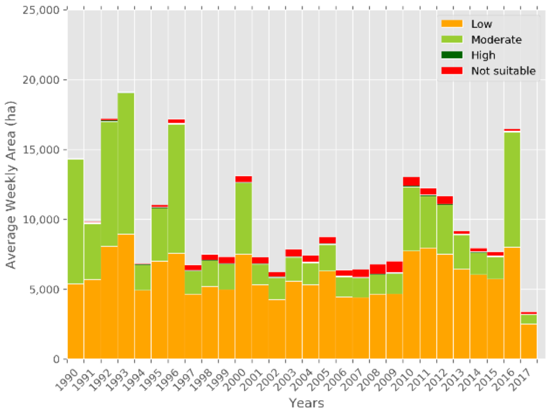


Mid Murray River catchment (y scale max 25,000)

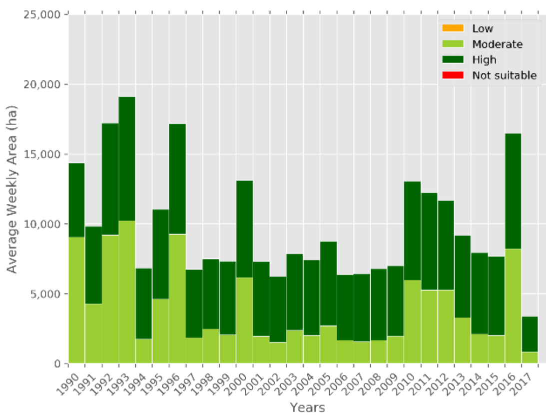
(a) Hydrological classes



(b) Larvae / YOY suitability

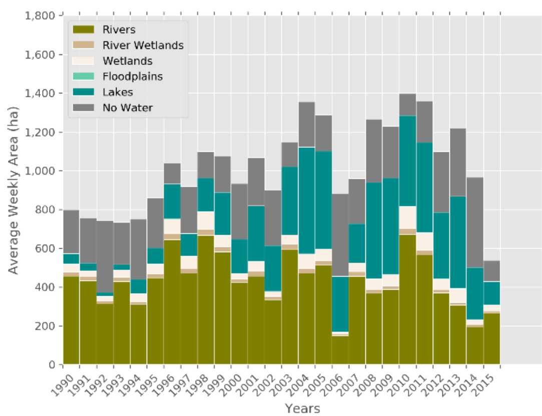


(c) Sub-adult / Adult suitability

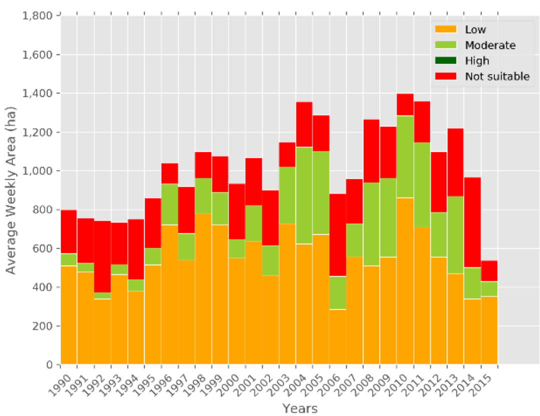


Moonie River catchment (y scale max 1,800)

(a) Hydrological classes



(b) Larvae / YOY suitability



(c) Sub-adult / Adult suitability

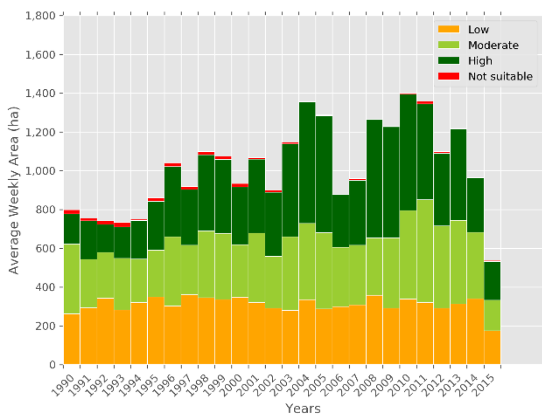
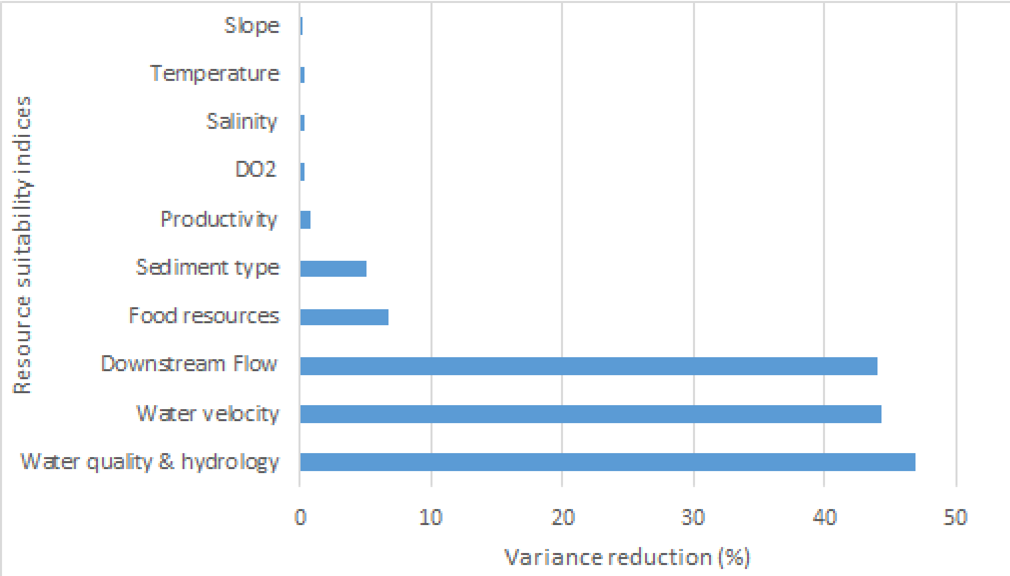


Figure 2.5.

Netica sensitivity analysis output showing the relative importance of each node in the two BBNs as measured by percentage variance reduction, with a greater reduction percentage indicating the variable is more important.

(a) Sub-adult/adult BBN



(b) Larvae/YOY BBN

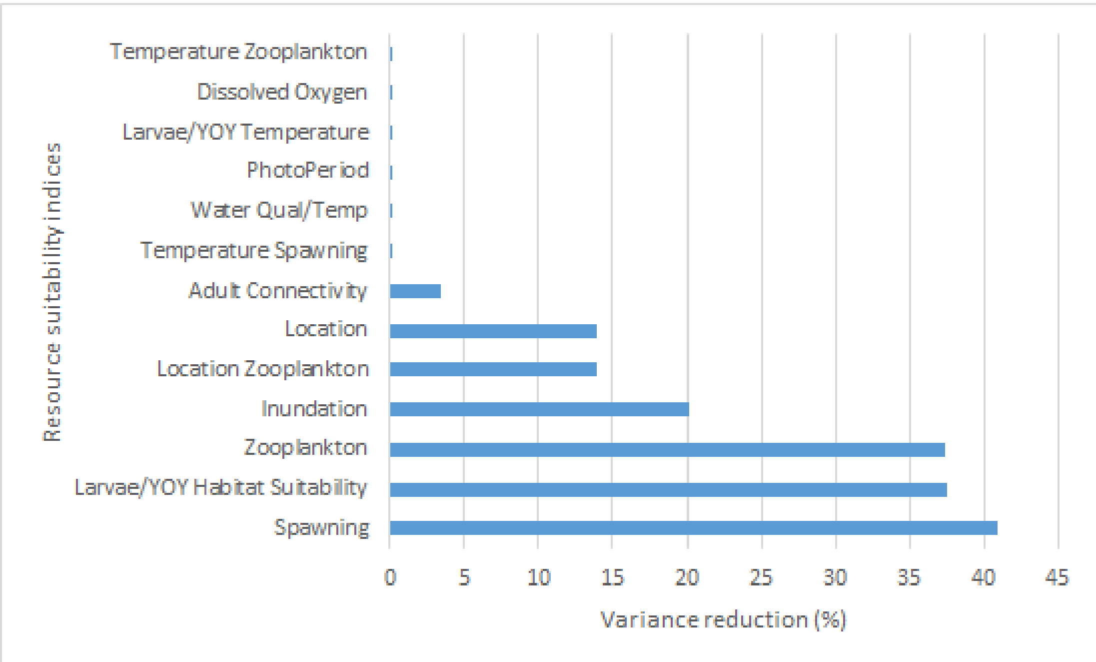
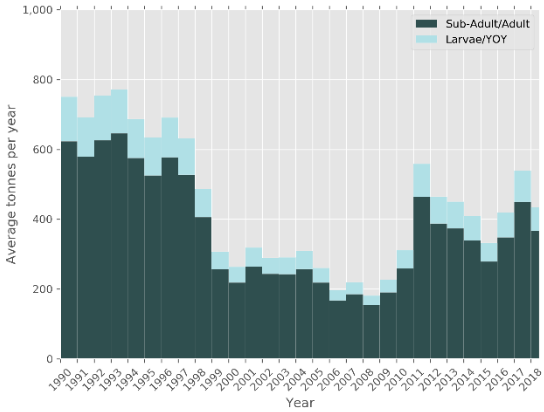


Figure 2.6.

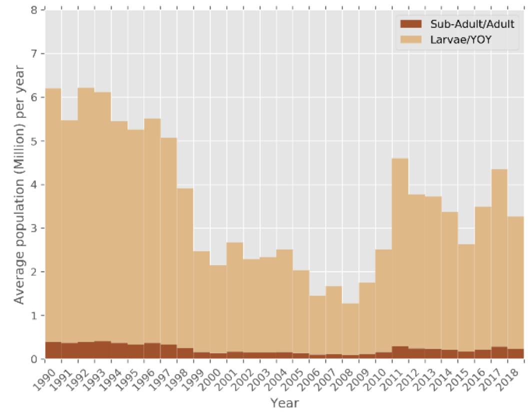
Time series stacked barcharts for each of the study catchments (a) the estimated average annual biomass of carp in the catchment; (b) the estimated average annual population size (number of individual fish). Note that due to the variability in each case-study catchment, the y-axes have different maximum values.

Glenelg River Catchment

(a) Average annual biomass

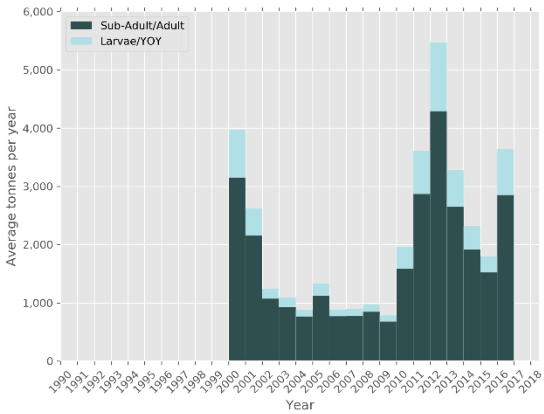


(b) Average annual population size

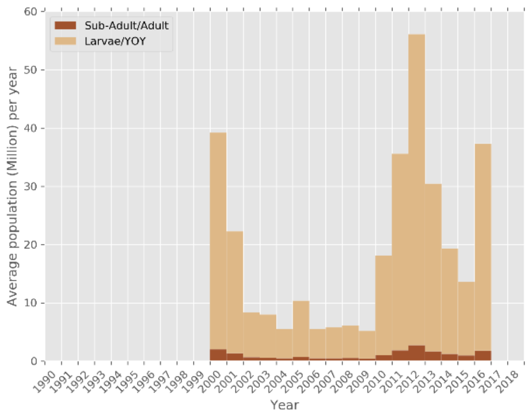


Lachlan River catchment

(a) Average annual biomass

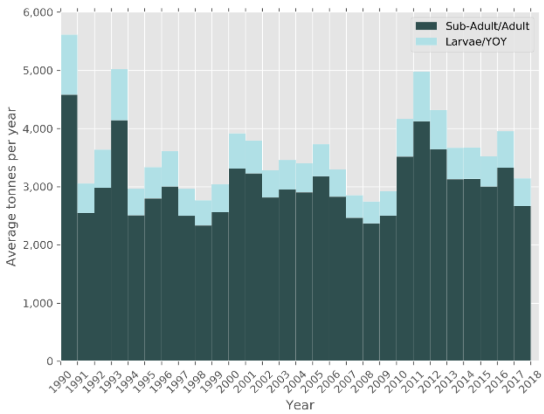


(b) Average annual population size

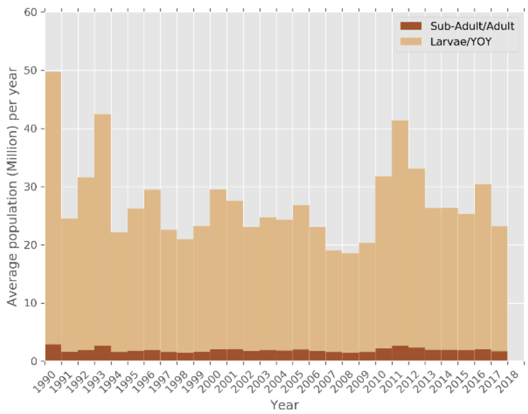


Lower Murray River catchment

(a) Average annual biomass

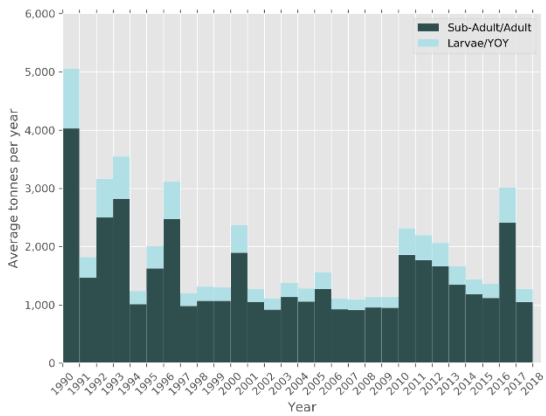


(b) Average annual population size

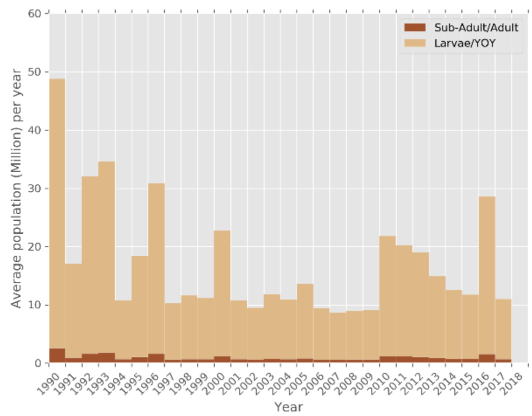


Mid Murray River catchment

(a) Average annual biomass

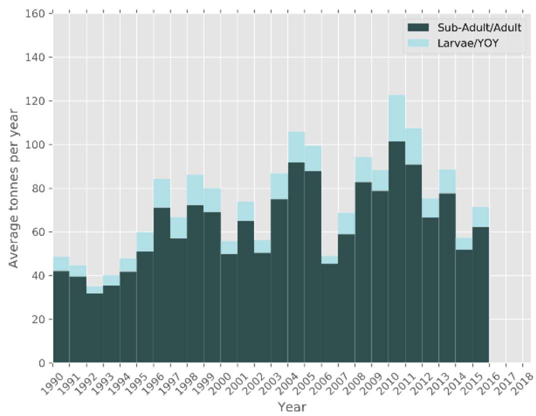


(b) Average annual population size



Moonie River catchment

(a) Average annual biomass



(b) Average annual population size

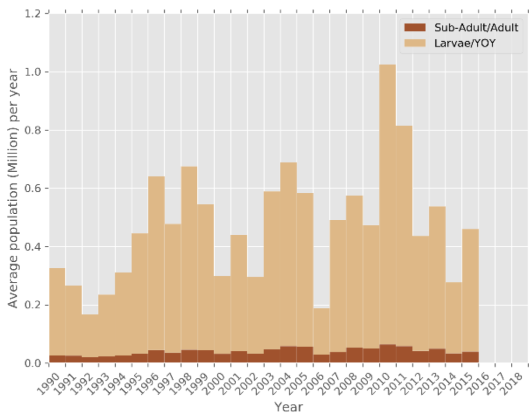
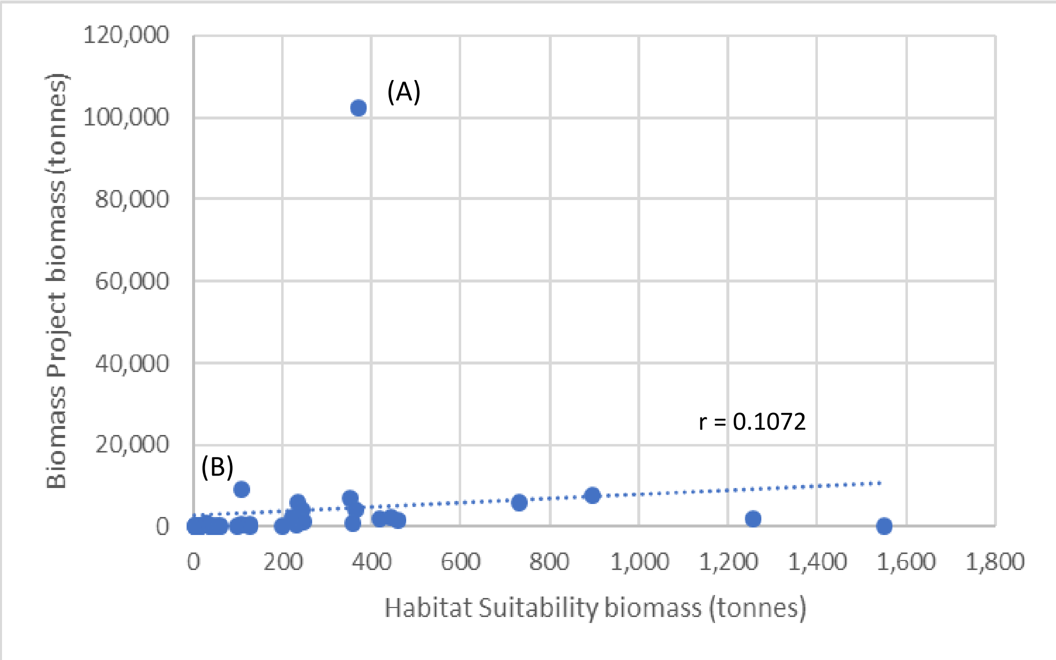


Figure 2.7.

Scatter plots showing the correlation between the habitat suitability derived estimates of the biomass (in tonnes) in each of the 32 zones for week 20 of 2011 (x-axis) and the estimate provided by the Biomass Project for the same period (y-axis). (a) unadjusted for the estimated waterbody area; and (b) adjusted for the estimated waterbody area. In Figure (a), the outliers indicated by A and B correspond to Zone 2 in the Mid-Murray (Barmah Forest) and Zone 8 in Lachlan (Willandra Creek)

(a) Unadjusted



(b) Adjusted

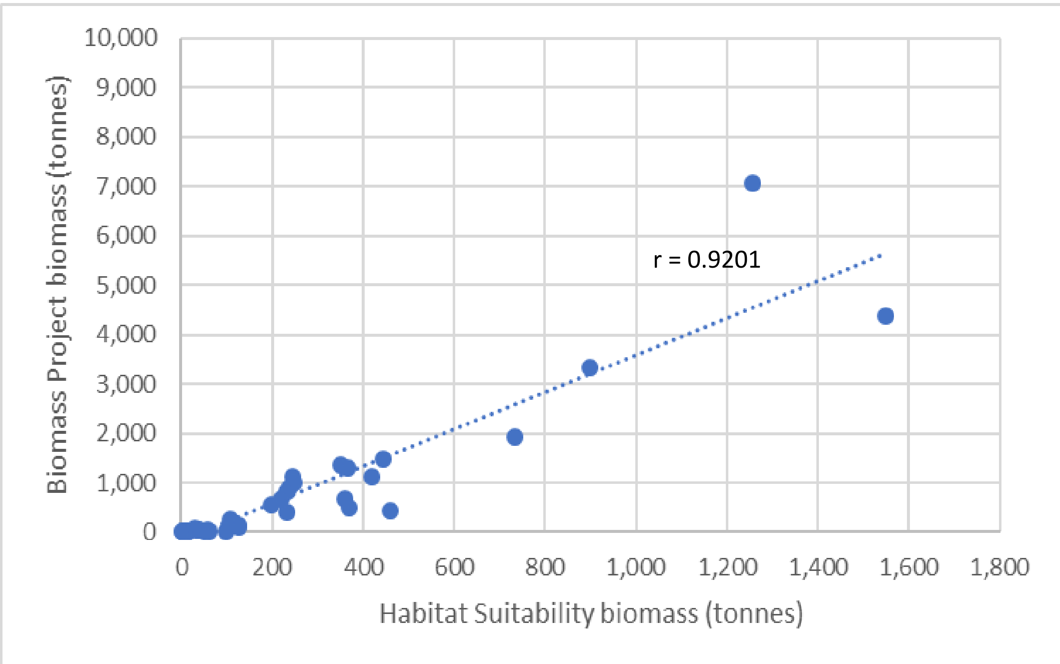
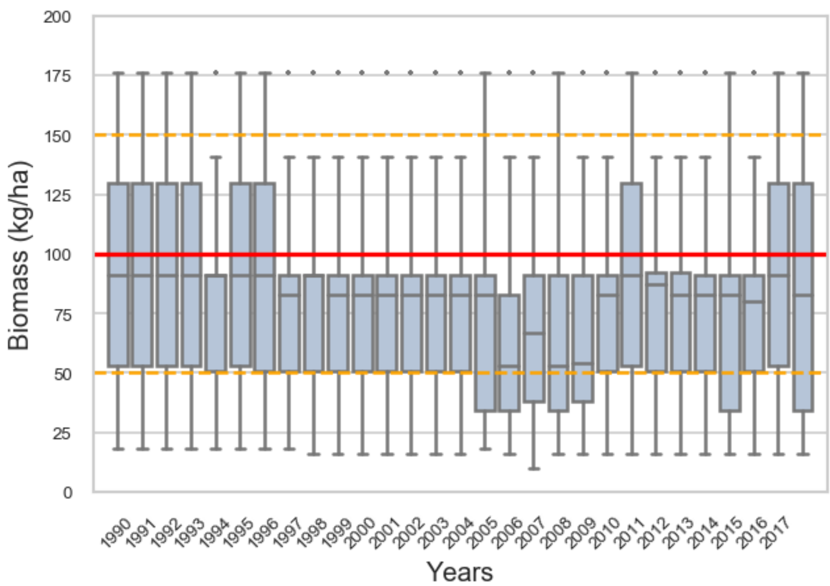


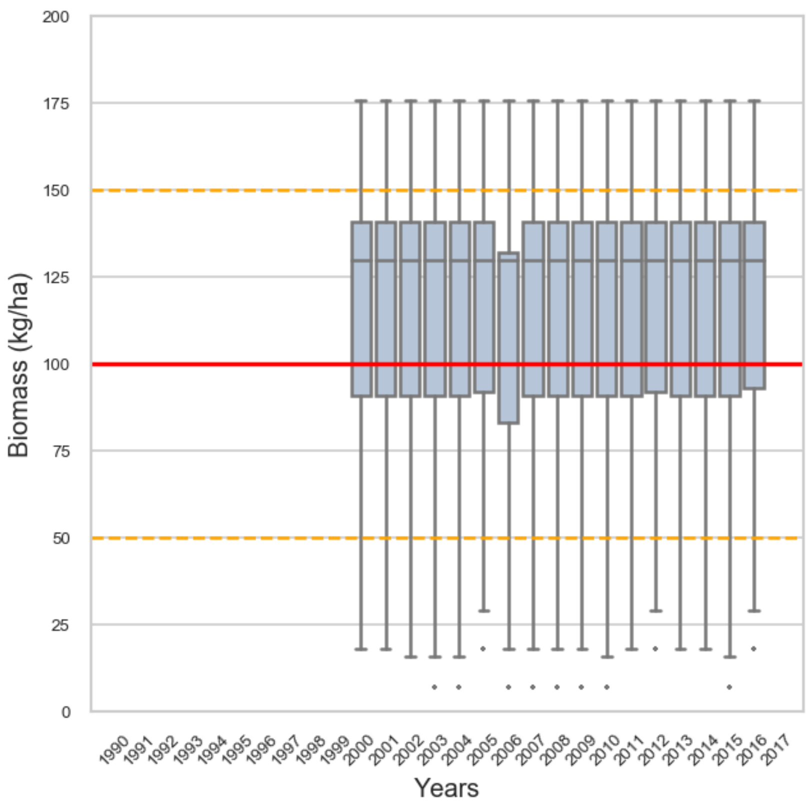
Figure 2.8

Time series of boxplots of the biomass density (kg/ha) for each of the study catchments in relation to the three identified thresholds at which carp are hypothesised to induce ecological damage (50 kg/ha, 100 kg/ha and 150 kg/ha).

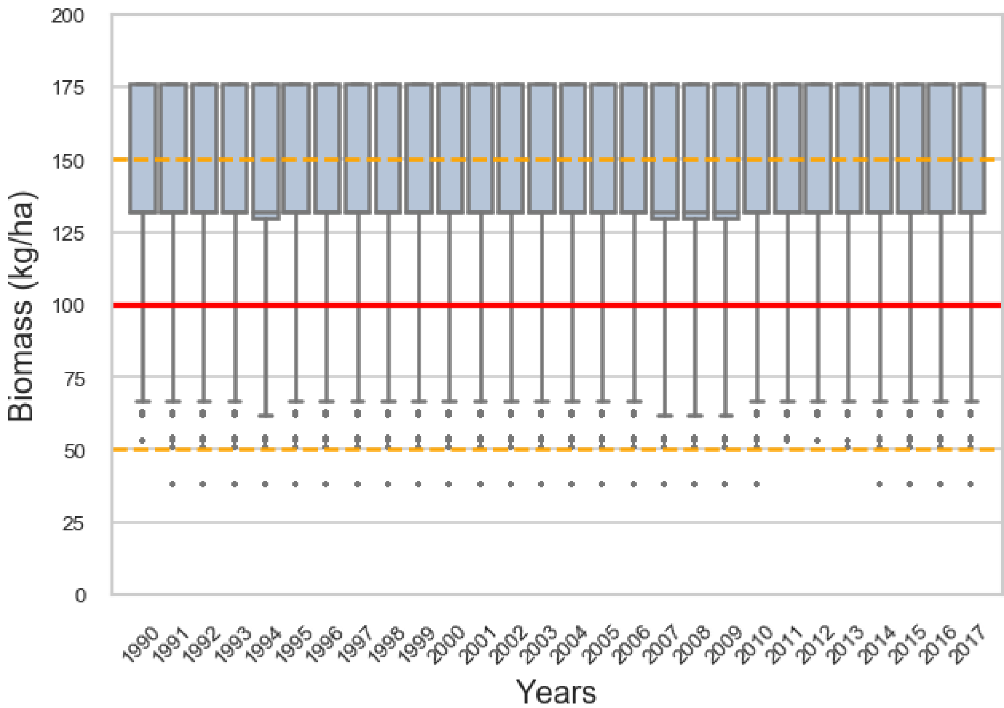
a. Glenelg River catchment



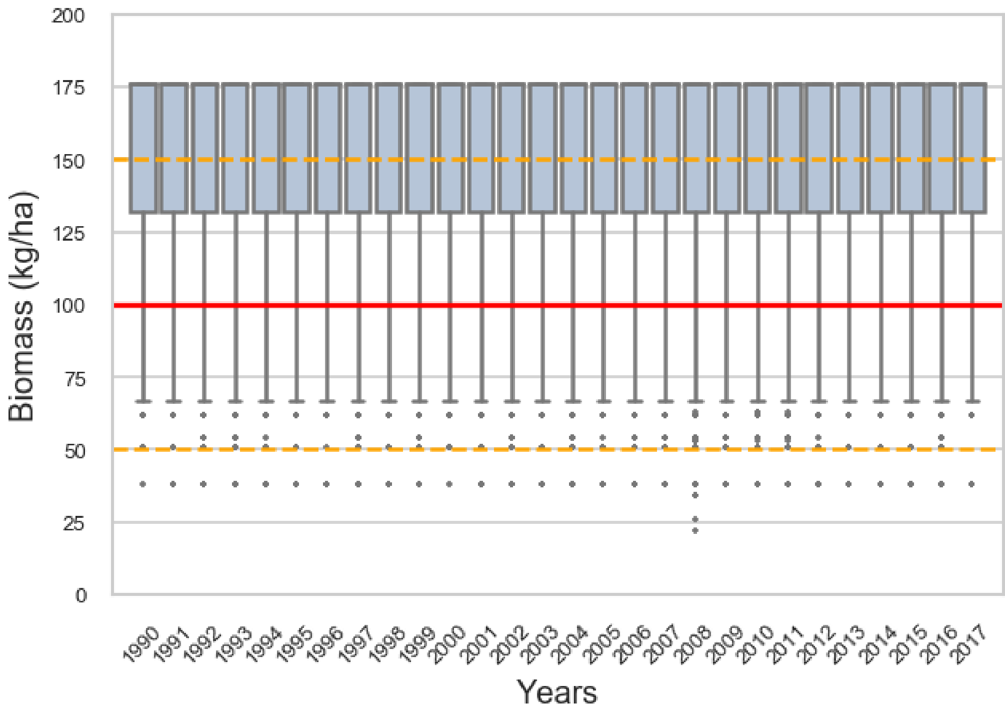
b. Lachlan River catchment



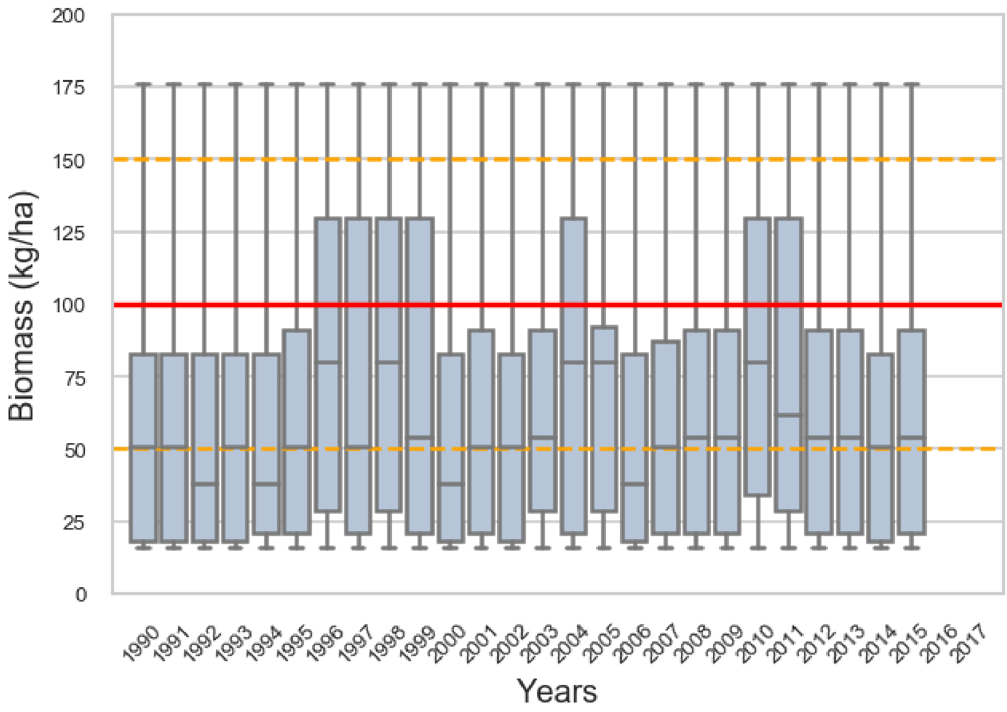
c. Lower Murray River catchment



d. Mid Murray River catchment



__e. Moonie River Catchment__



Supplementary figures

Figure S1

BBN workshop output in which the experts identified the key environmental variables (KEV) associated with habitat suitability for carp and how they influence each other. While this influence diagram subsequently underwent numerous revisions, including splitting the BBN into separate networks for subadults/adults and larvae/YOY, the basic role of these KEVs is apparent in the final BBN shown in Figure 2.3.

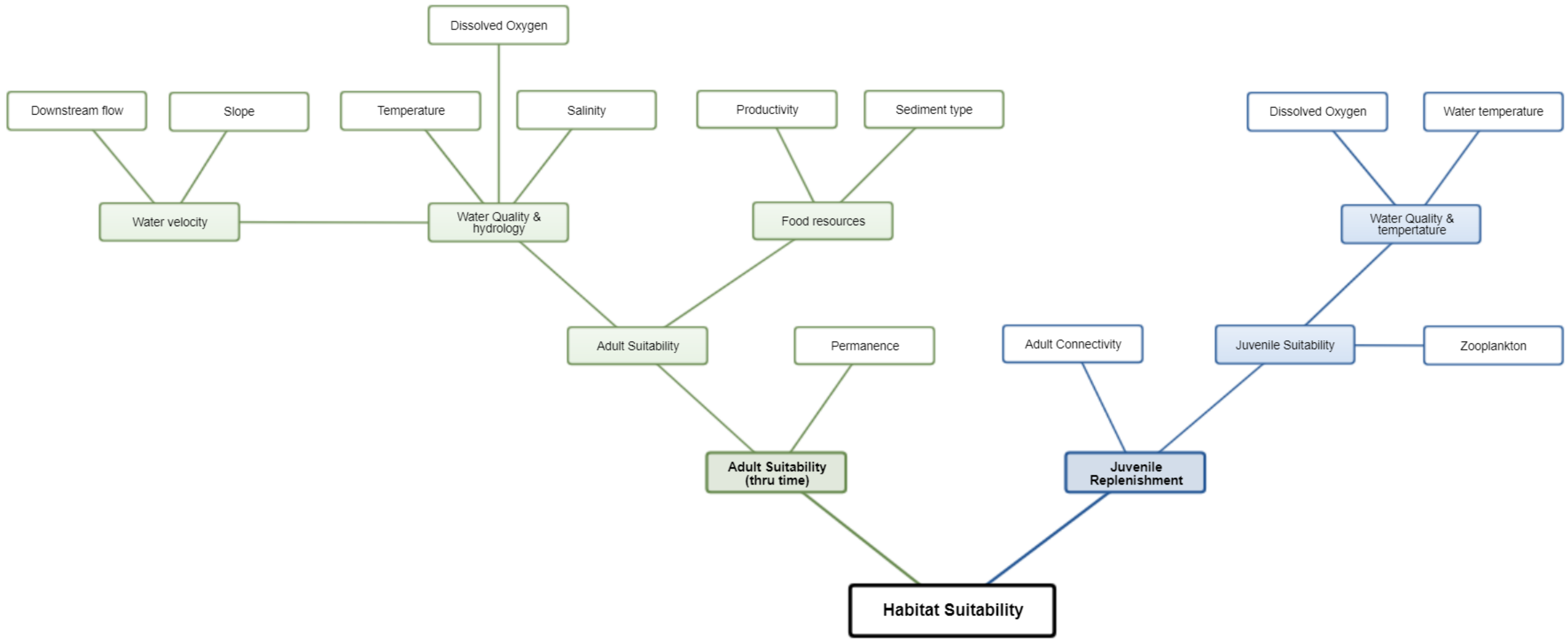
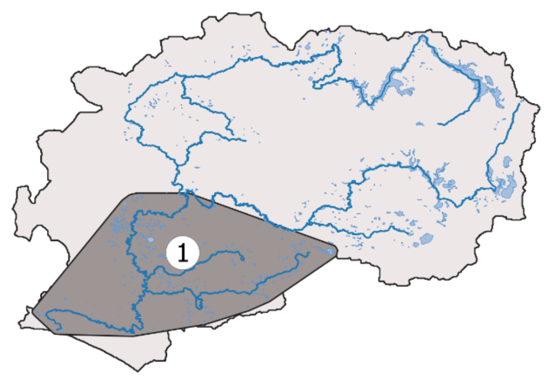


Figure S2

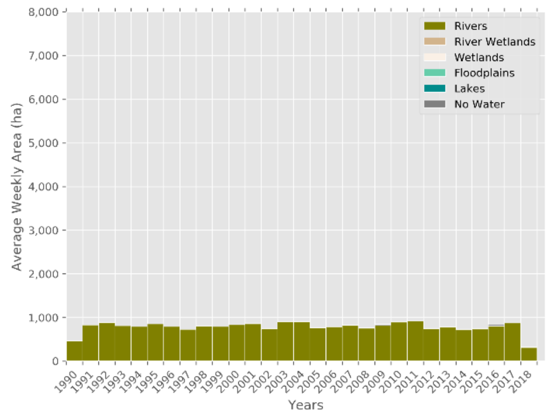
Time series plots at the zonal level for habitat suitability areas, habitat suitability for adults/subadults, biomass density and population sizes.

a. Glenelg River catchment

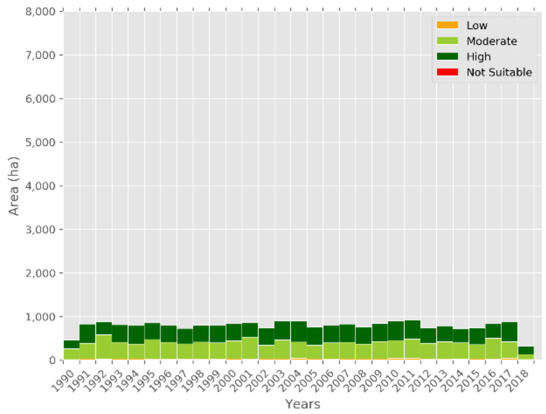
Zone 1 - Glenelg River below Wannon River, Crawford River and Stokes River



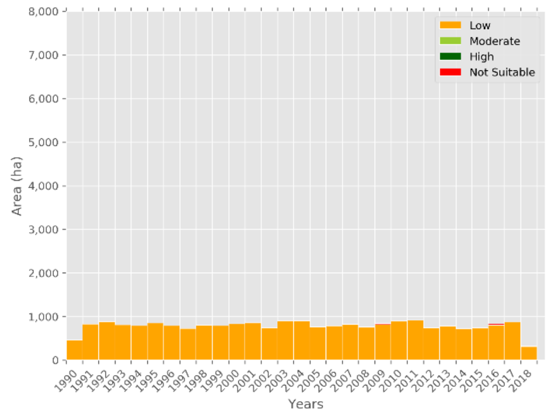
(a) Hydrological classes

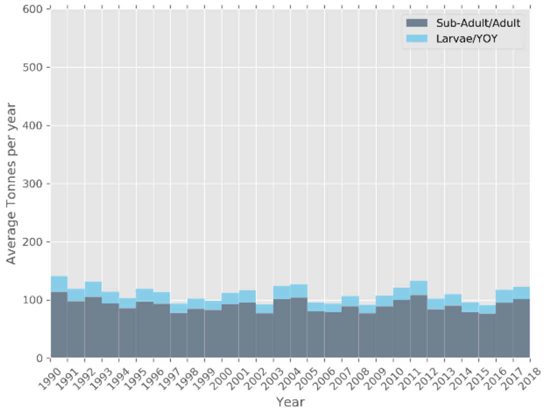
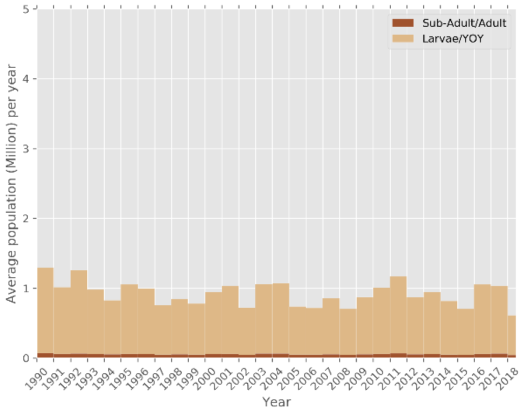


(b) Sub-adult/adult suitability

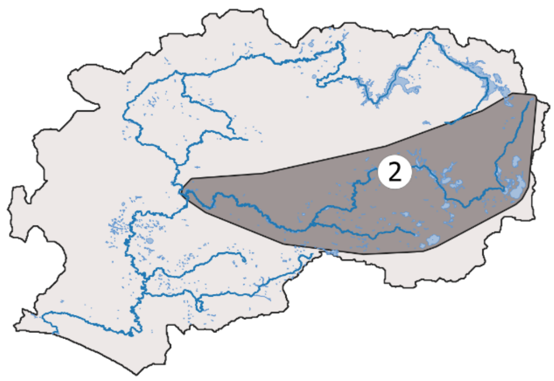


(c) Larvae / YOY suitability

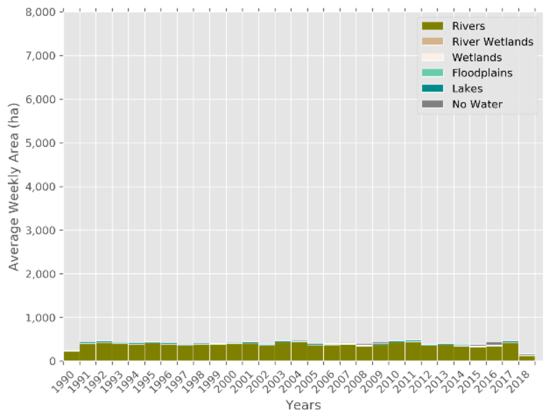


(d) Average annual biomass	(e) Average annual population size
	

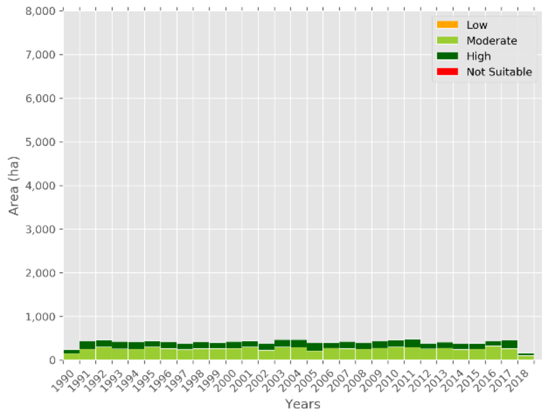
Zone 2 – Wannon River – Lake Hamilton



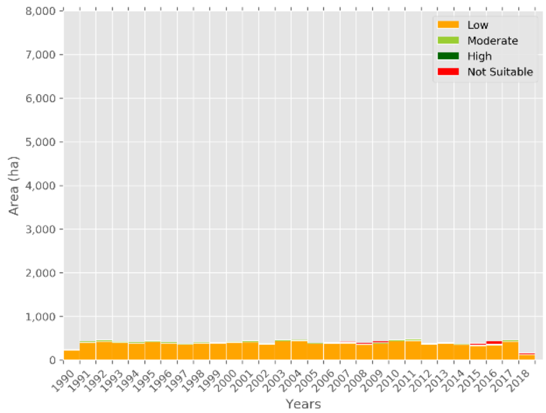
(a) Hydrological classes



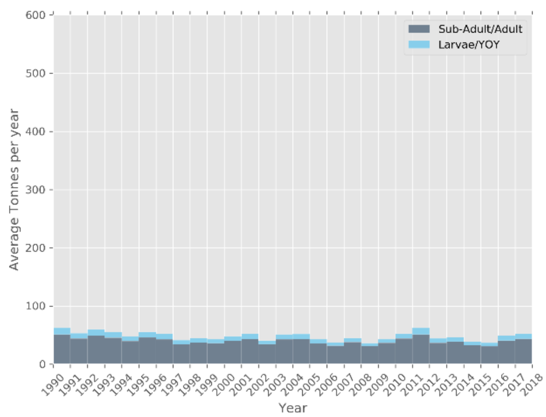
(b) Sub-adult/adult suitability



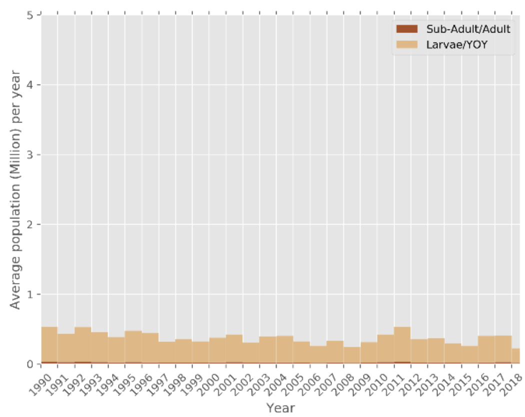
(c) Larvae / YOY suitability



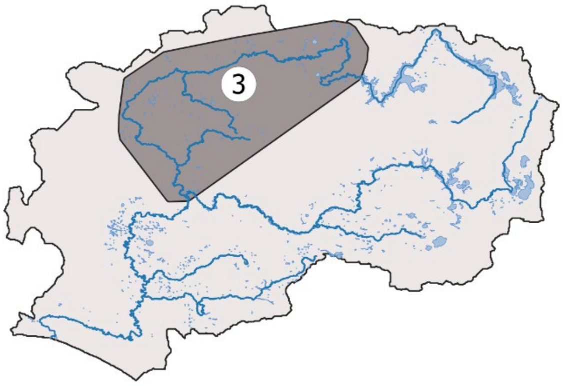
(d) Average annual biomass



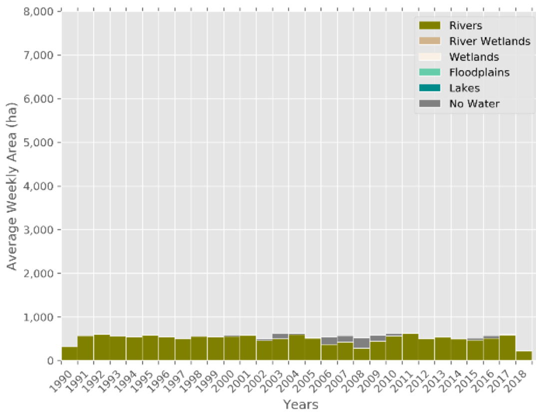
(e) Average annual population size



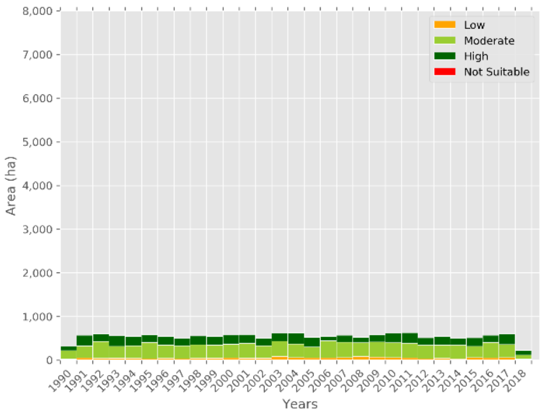
Zone 3 - Glenelg River below Rocklands Reservoir to Wannon River, Wando River and Chetwynd River



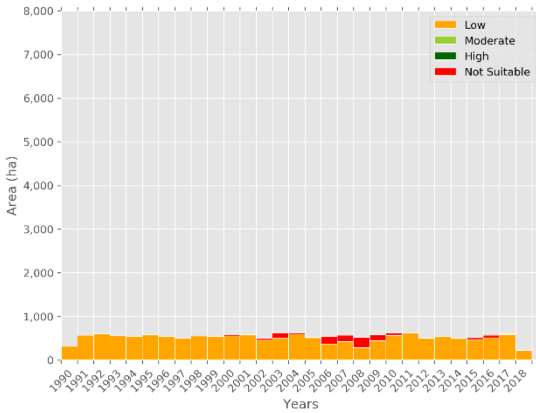
(a) Hydrological classes



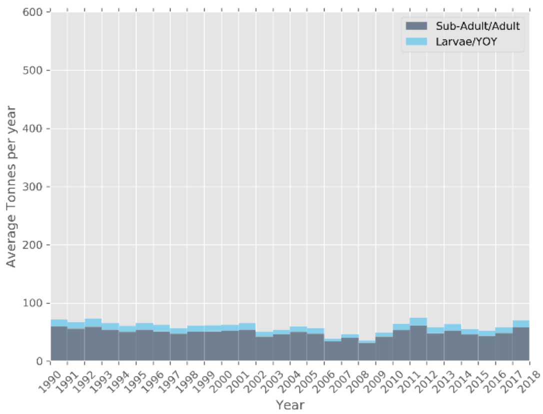
(b) Sub-adult/adult suitability



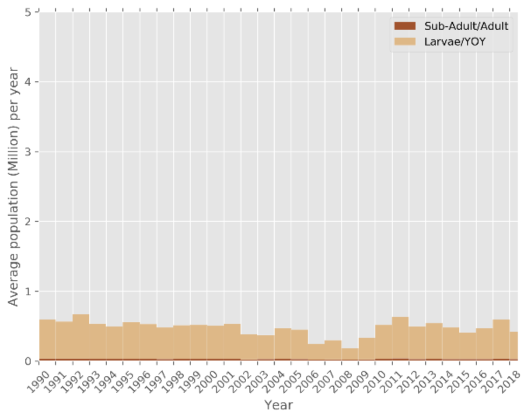
(c) Larvae / YOY suitability



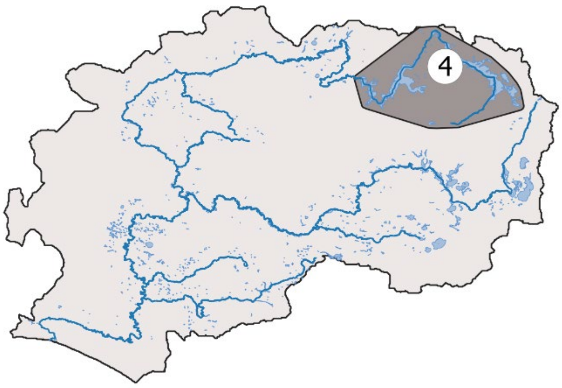
(d) Average annual biomass



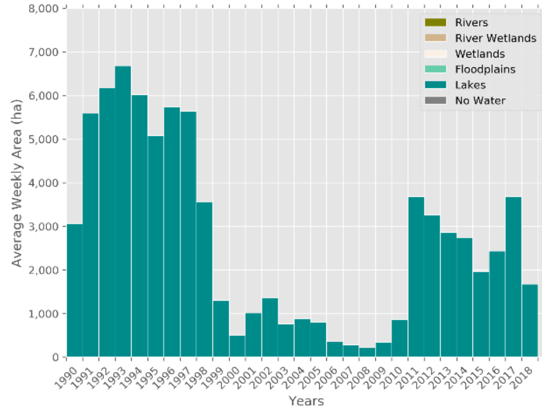
(e) Average annual population size



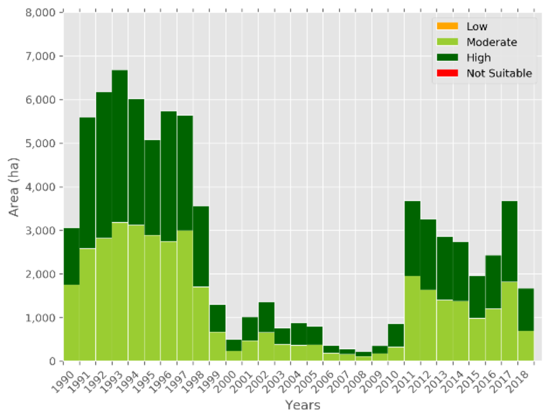
Zone 4 - Rocklands Reservoir and Glenelg River



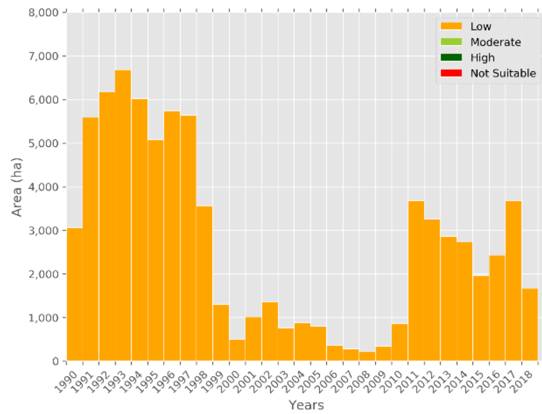
(a) Hydrological classes



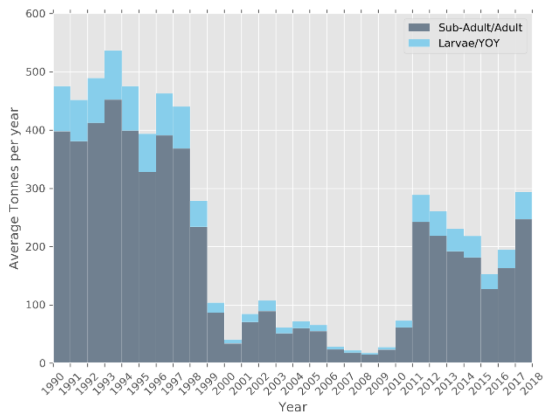
(b) Sub-adult/adult suitability



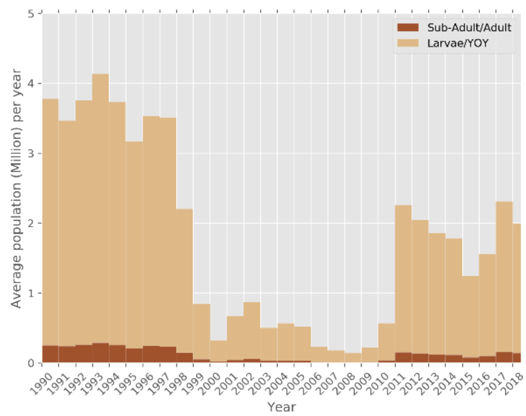
(c) Larvae / YOY suitability



(d) Average annual biomass

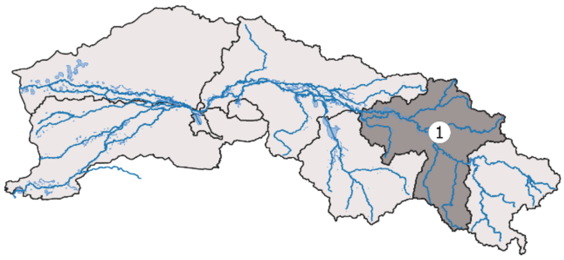


(e) Average annual population size

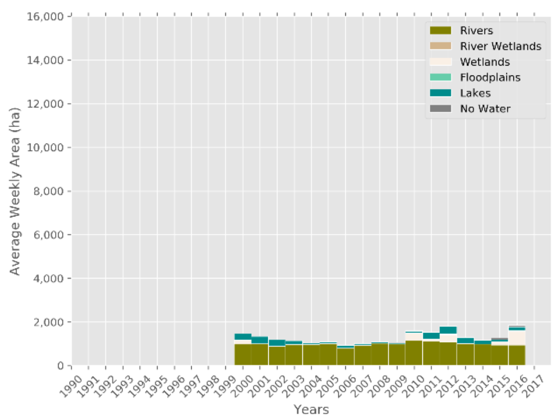


b. Lachlan River catchment

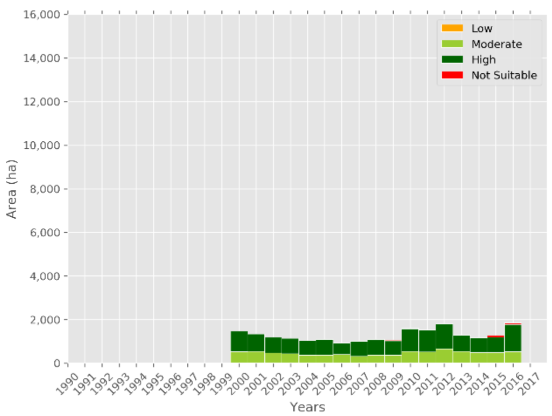
Zone 1 - Wyangala Dam to Jemalong Weir



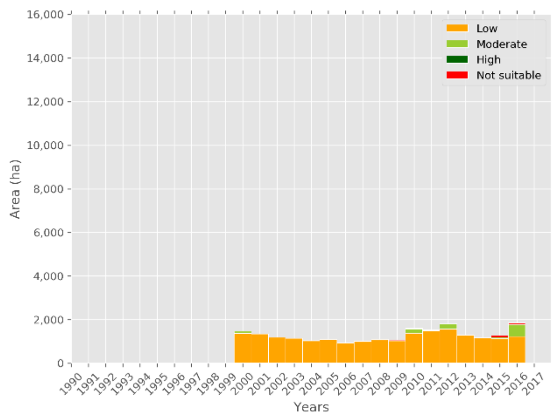
(a) Hydrological classes



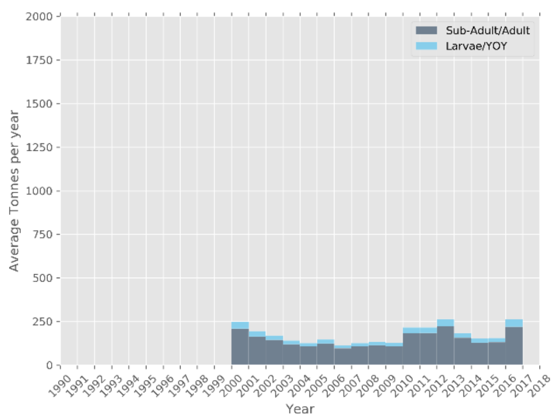
(b) Sub-adult/adult suitability



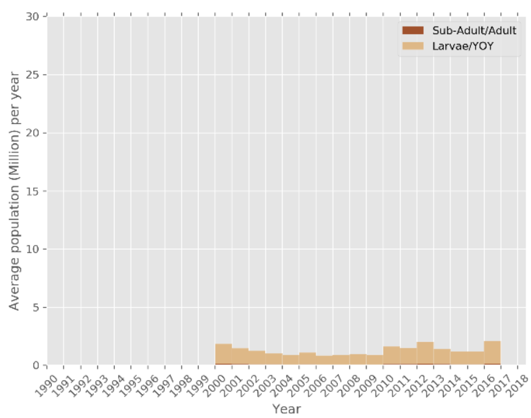
(c) Larvae / YOY suitability



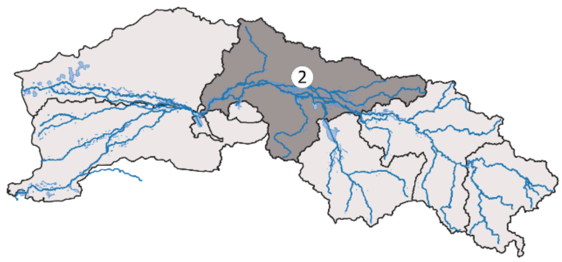
(d) Average annual biomass



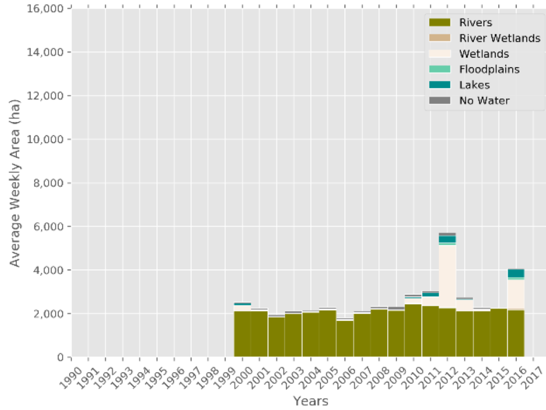
(e) Average annual population size



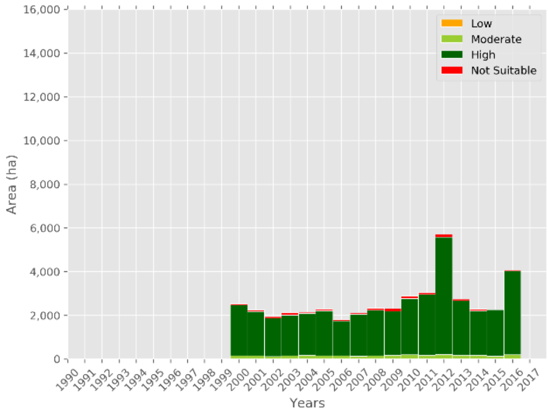
Zone 2 - Jemalong Weir to Brewster Weir



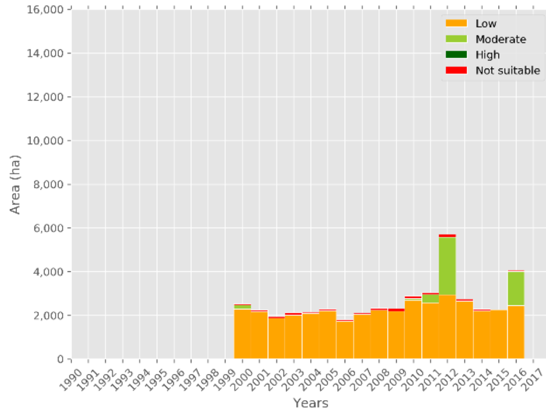
(a) Hydrological classes



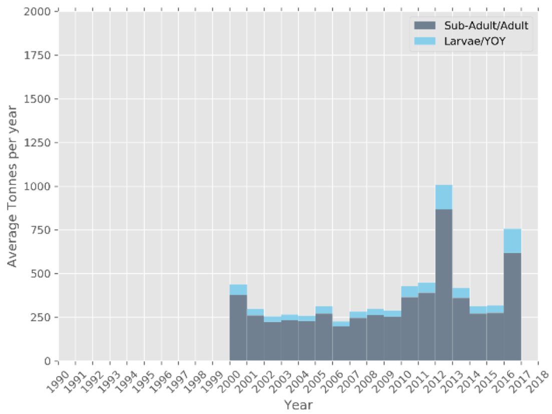
(b) Sub-adult/adult suitability



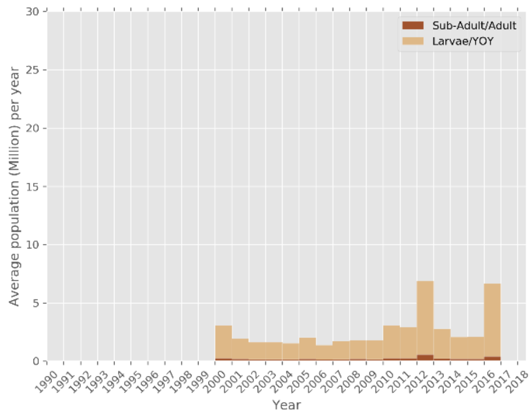
(c) Larvae / YOY suitability



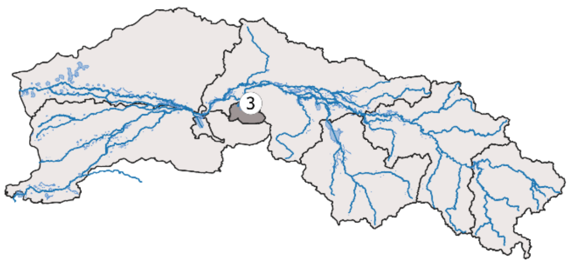
(d) Average annual biomass



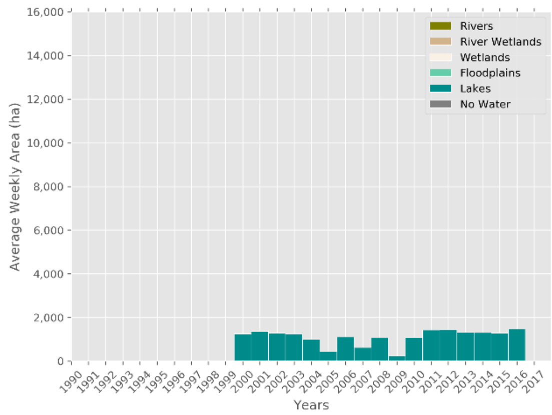
(e) Average annual population size



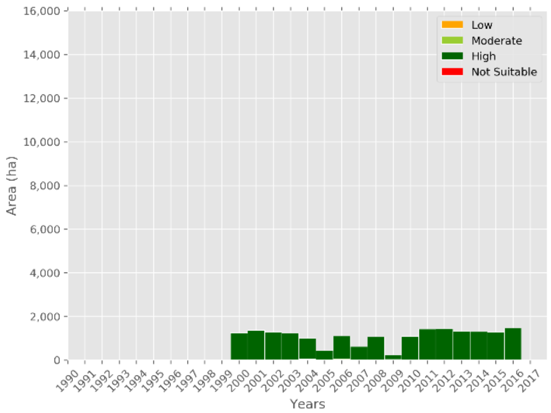
Zone 3 - Lake Cargelligo



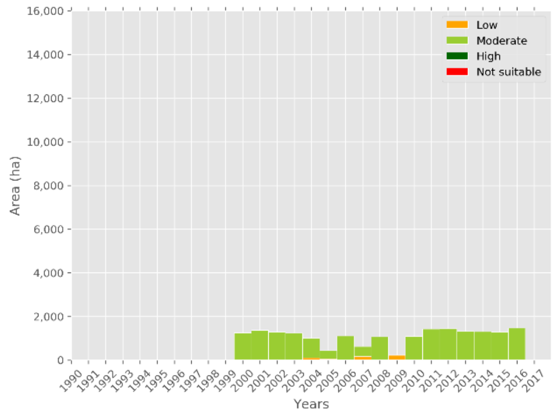
(a) Hydrological classes



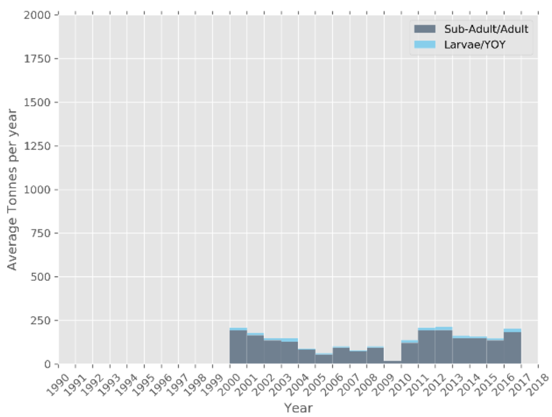
(b) Sub-adult/adult suitability



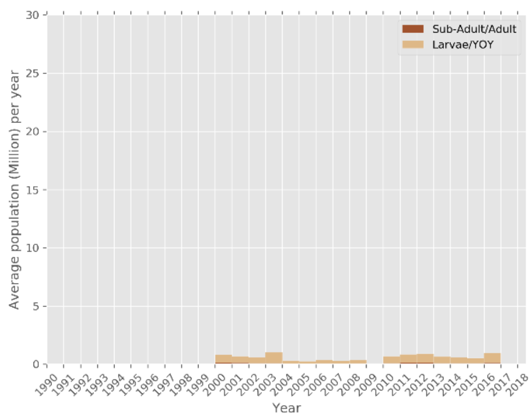
(c) Larvae / YOY suitability



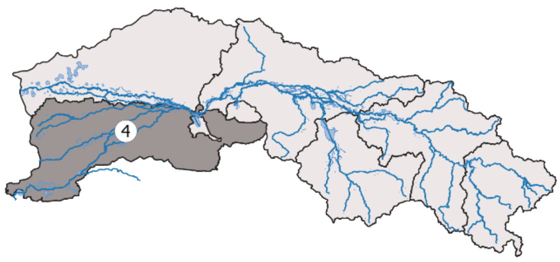
(d) Average annual biomass



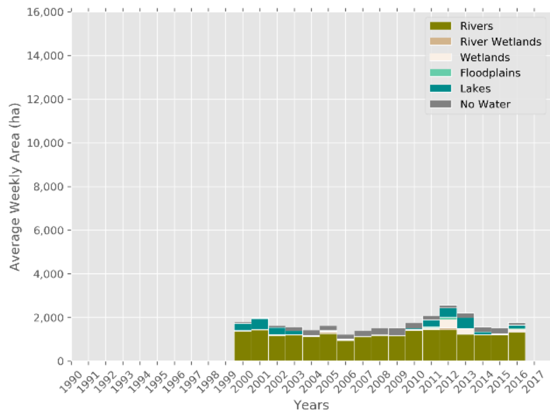
(e) Average annual population size



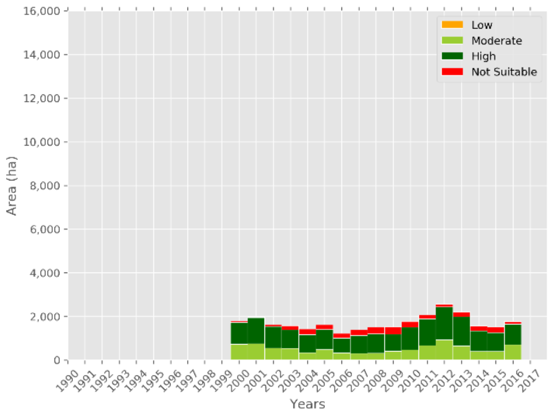
Zone 4 - Brewster Weir to Great Cumbung Swamp



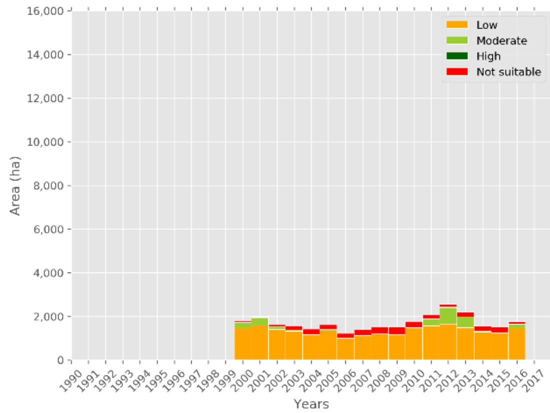
(a) Hydrological classes



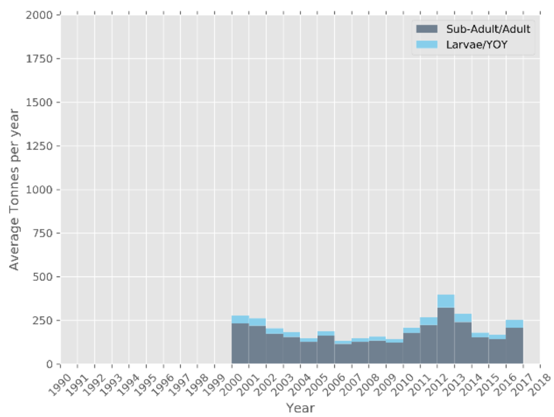
(b) Sub-adult/adult suitability



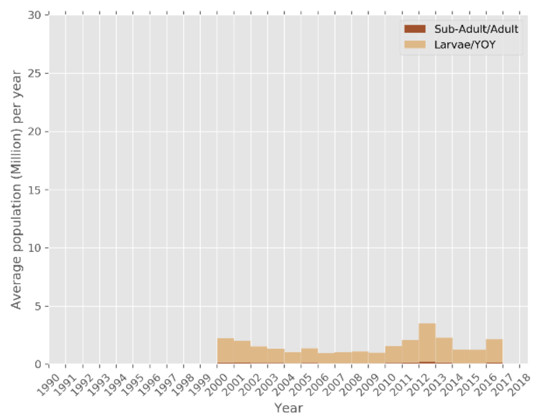
(c) Larvae / YOY suitability



(d) Average annual biomass

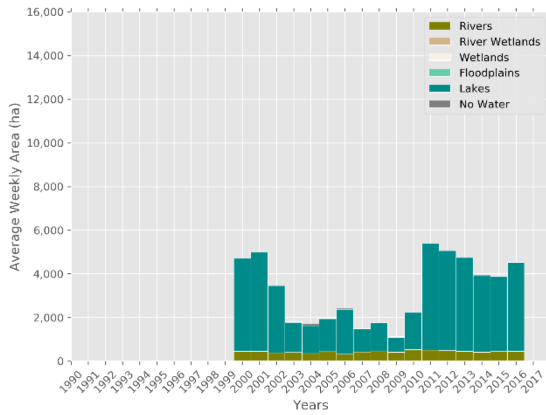


(e) Average annual population size

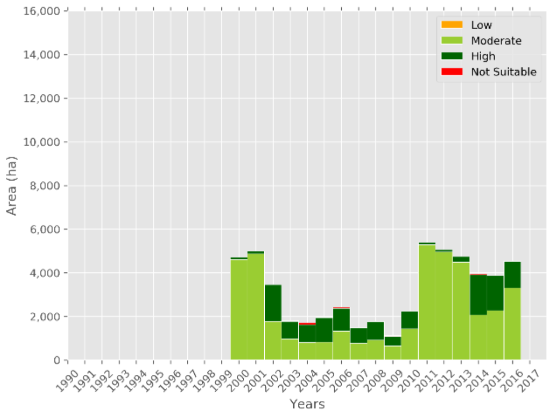


Zone 5 - Upstream of Wyangala Dam wall

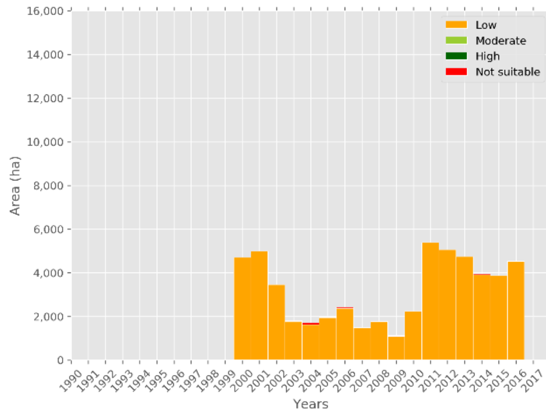
(a) Hydrological classes



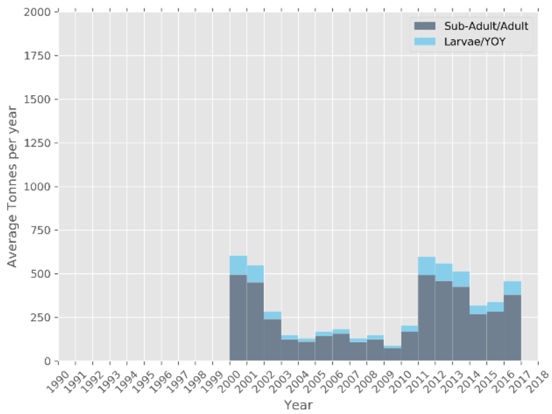
(b) Sub-adult/adult suitability



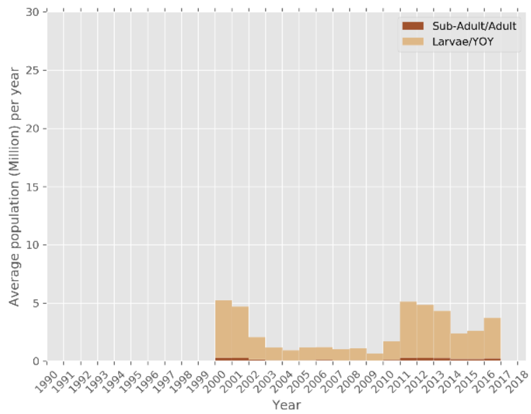
(c) Larvae / YOY suitability



(d) Average annual biomass

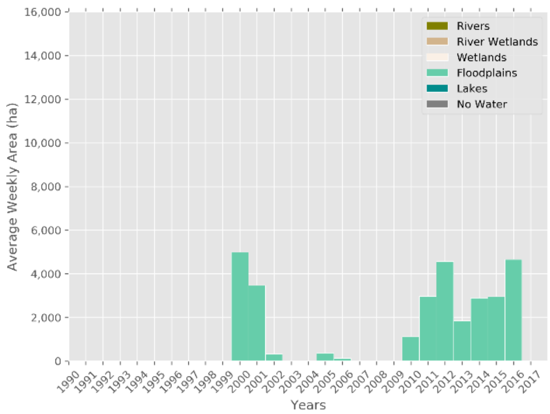


(e) Average annual population size

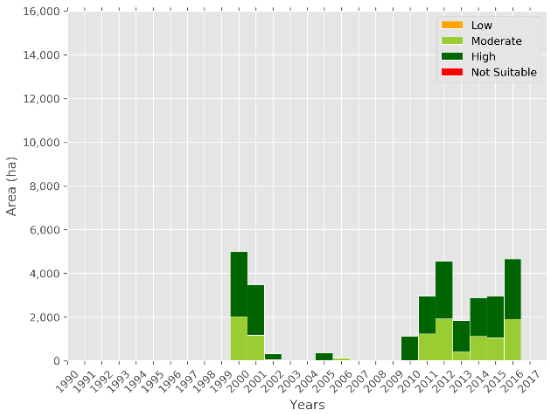


Zone 6 - Lake Brewster

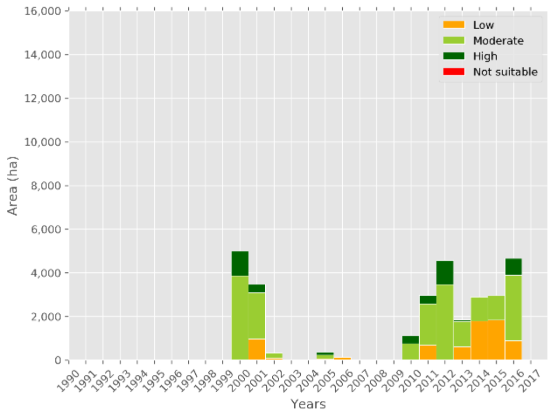
(a) Hydrological classes



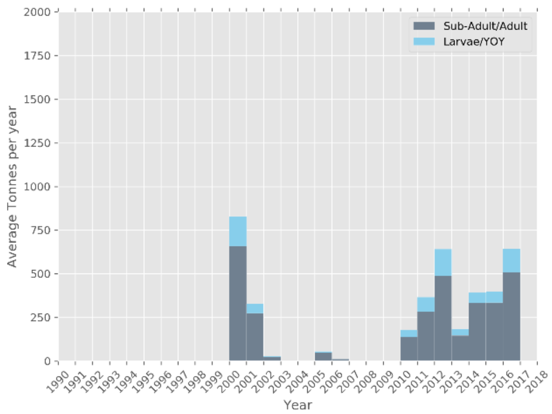
(b) Sub-adult/adult suitability



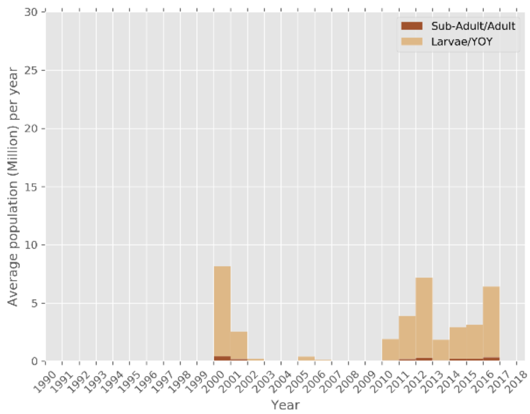
(c) Larvae / YOY suitability



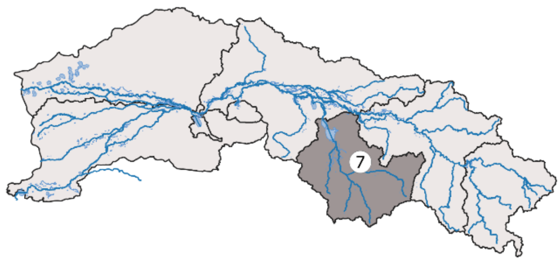
(d) Average annual biomass



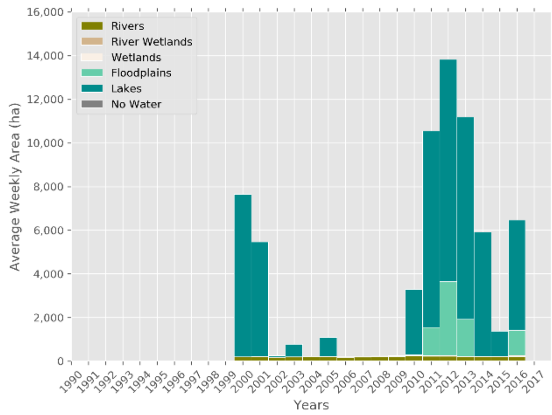
(e) Average annual population size



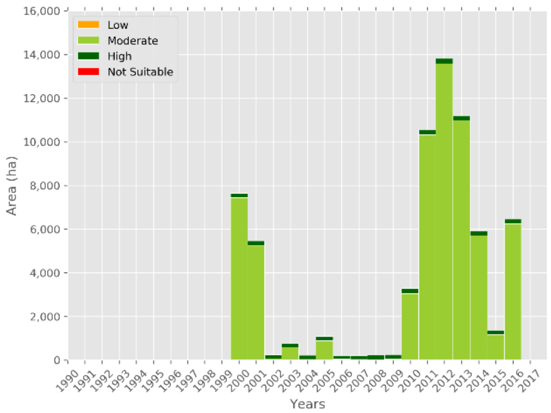
Zone 7 - Lake Cowal and upper drainage region



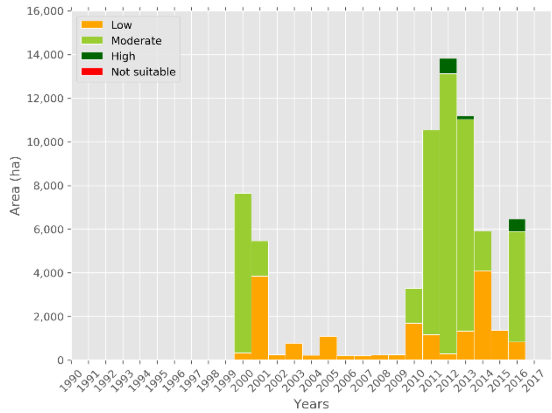
(a) Hydrological classes



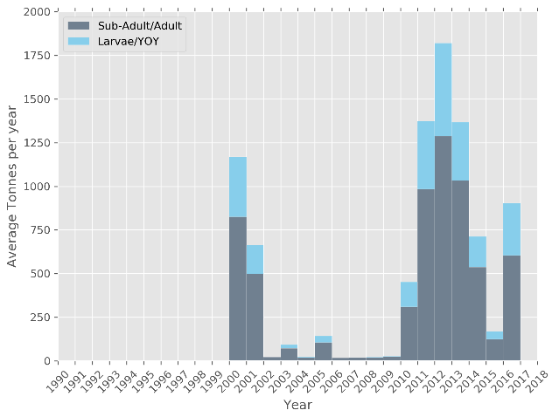
(b) Sub-adult/adult suitability



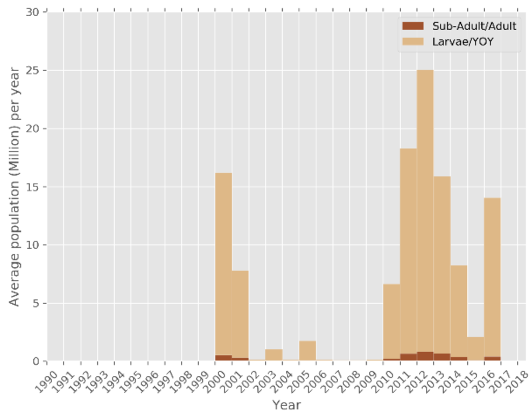
(c) Larvae / YOY suitability



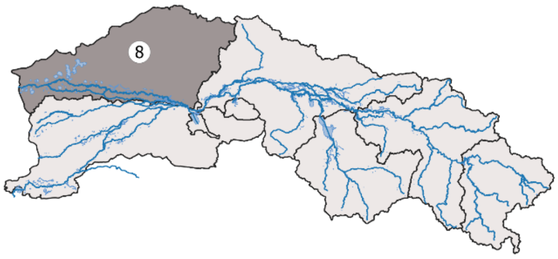
(d) Average annual biomass



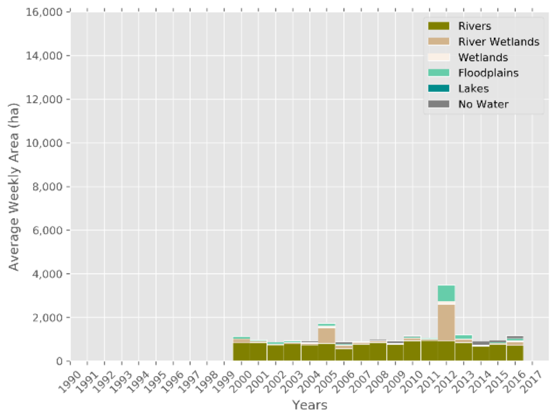
(e) Average annual population size



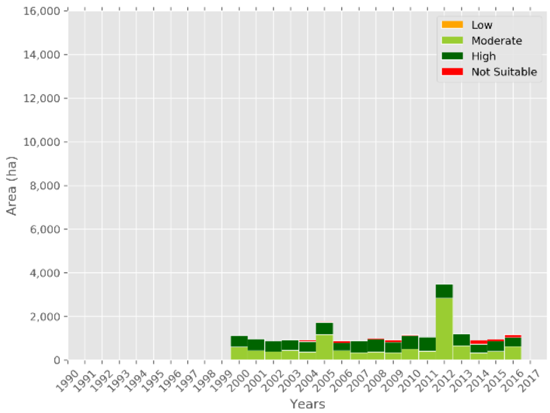
Zone 8 - Willandra Creek



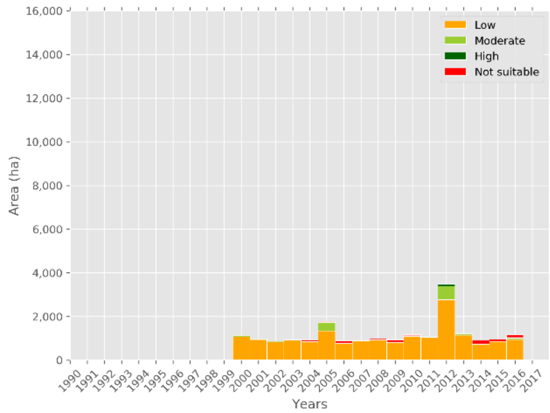
(a) Hydrological classes



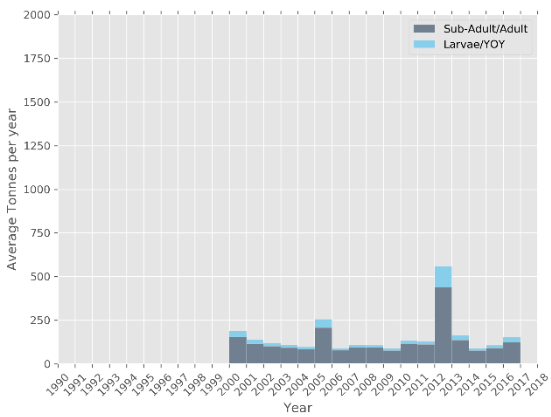
(b) Sub-adult/adult suitability



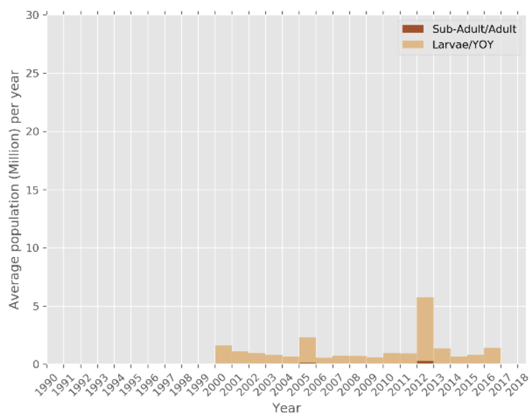
(c) Larvae / YOY suitability



(d) Average annual biomass

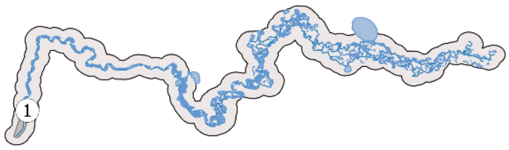


(e) Average annual population size



c. Lower Murray River catchment

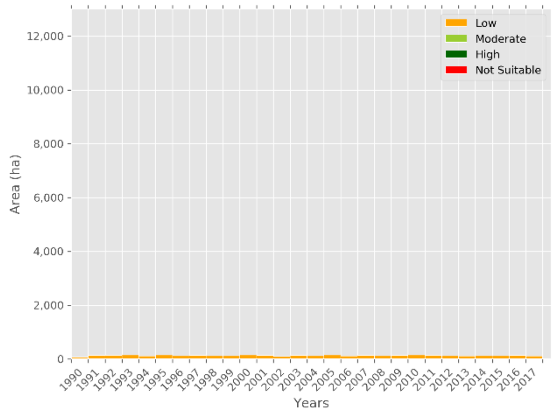
Zone - 1 Below Lock 1 (17.74kms)



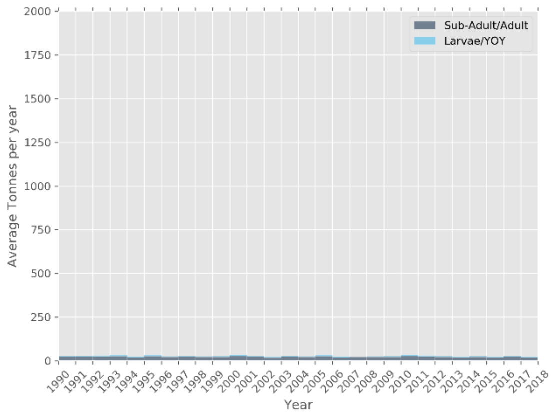
(a) Hydrological classes

(b) Sub-adult/adult suitability

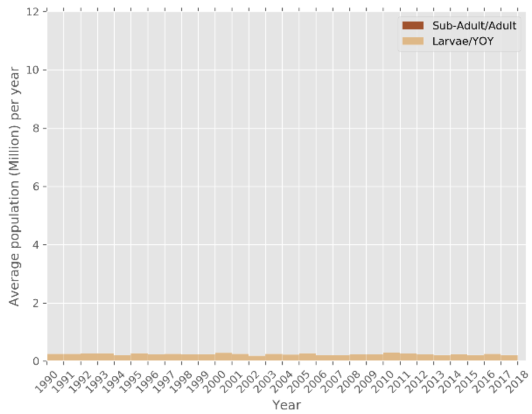
(c) Larvae / YOY suitability



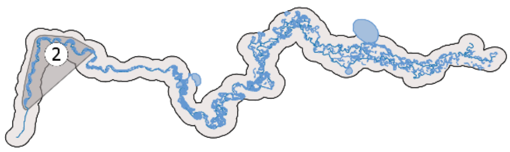
(d) Average annual biomass



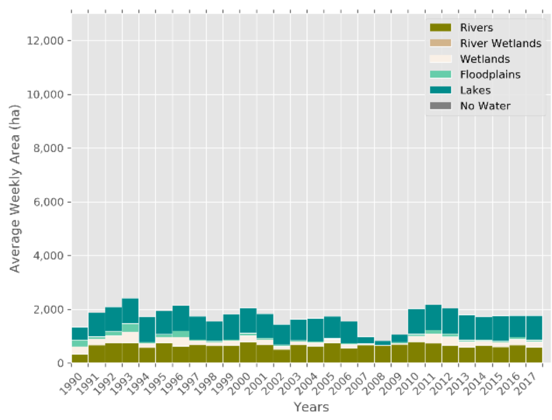
(e) Average annual population size



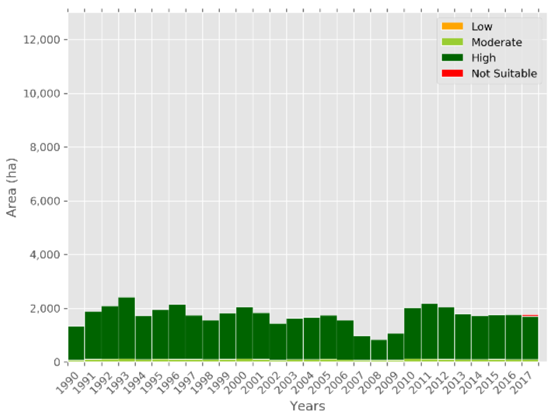
Zone 2 - Lock 2 to Lock 1



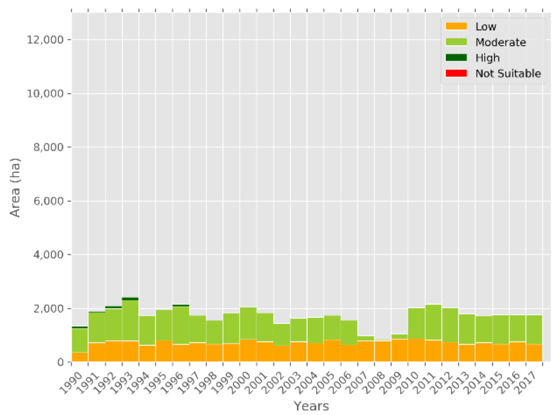
(a) Hydrological classes



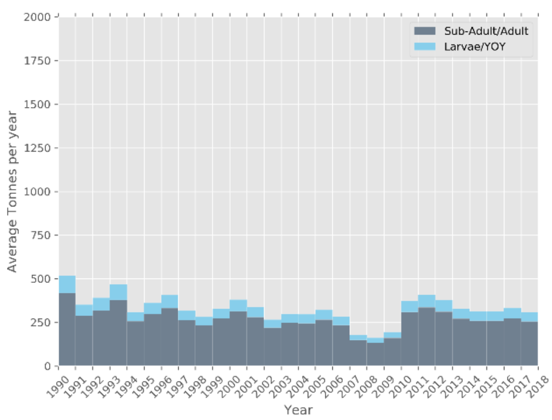
(b) Sub-adult/adult suitability



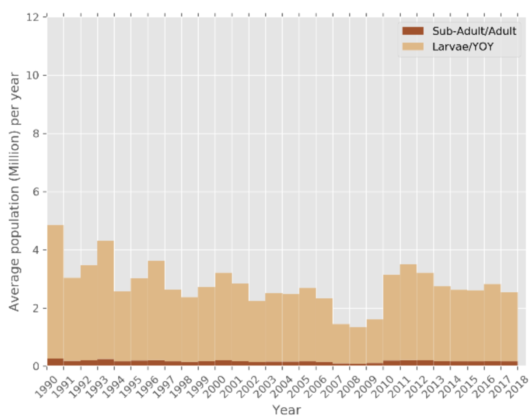
(c) Larvae / YOY suitability



(d) Average annual biomass

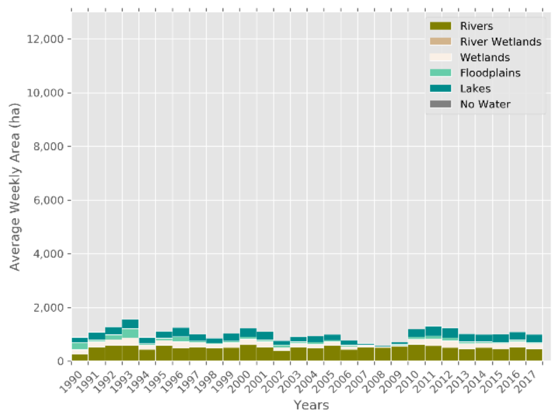


(e) Average annual population size

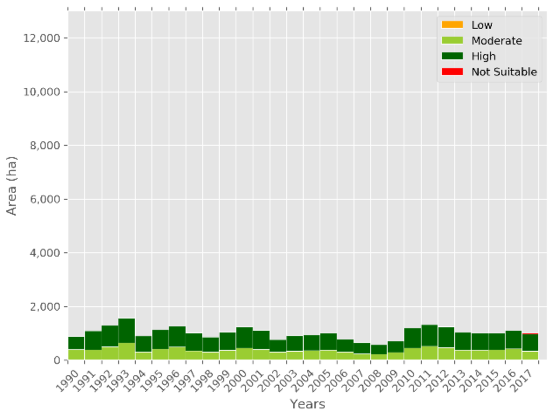


Zone 3 - Lock 3 to Lock 2

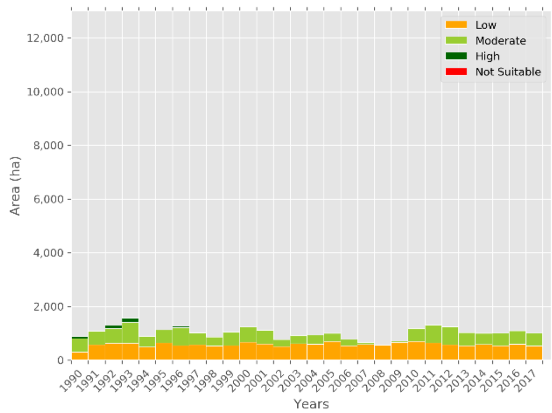
(a) Hydrological classes



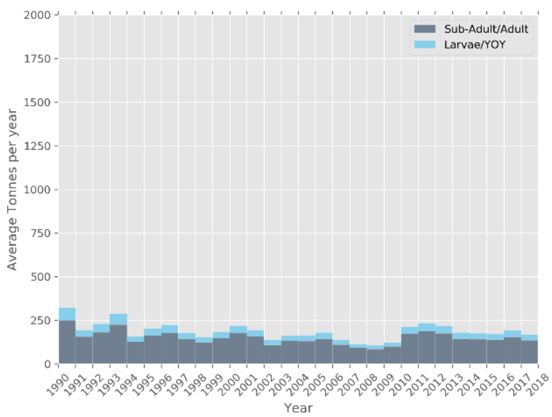
(b) Sub-adult/adult suitability



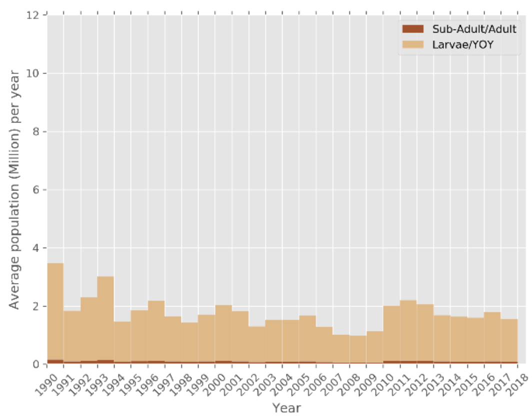
(c) Larvae / YOY suitability



(d) Average annual biomass

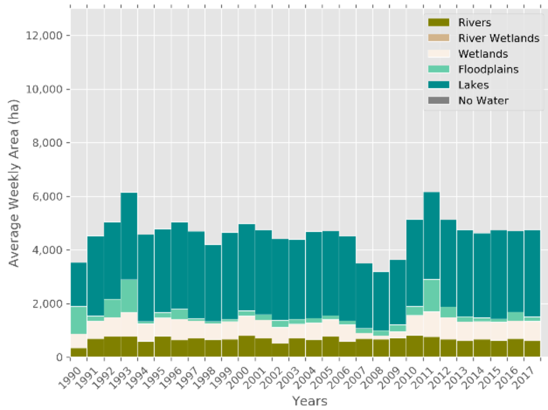


(e) Average annual population size

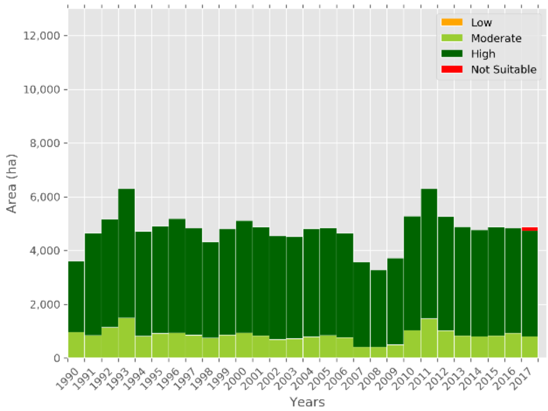


Zone 4 - Lock 4 to Lock 3 (Lake Bonney)

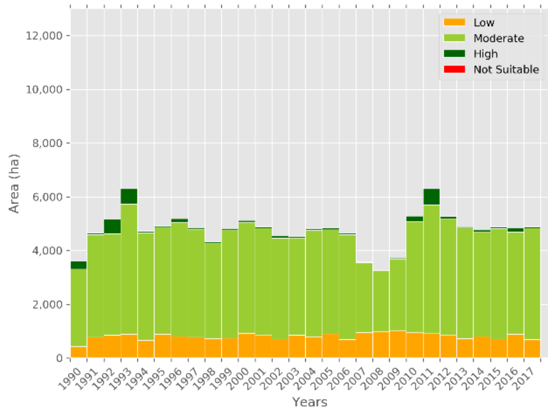
(a) Hydrological classes



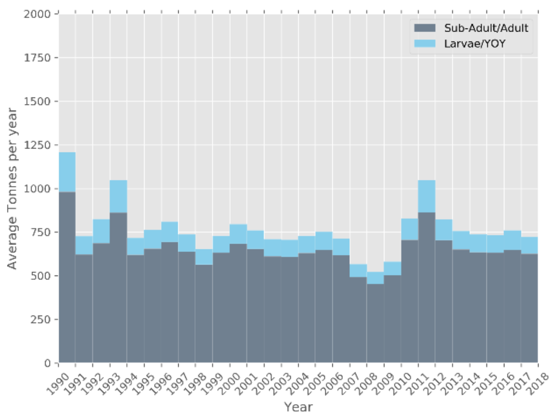
(b) Sub-adult/adult suitability



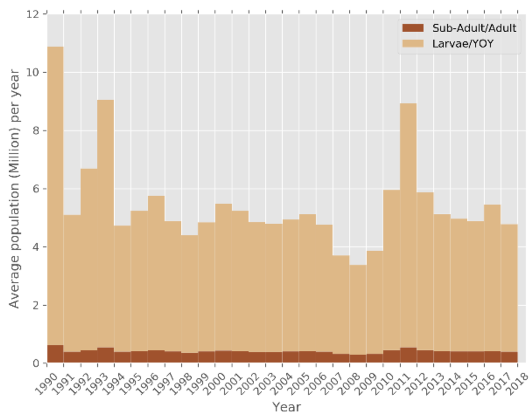
(c) Larvae / YOY suitability

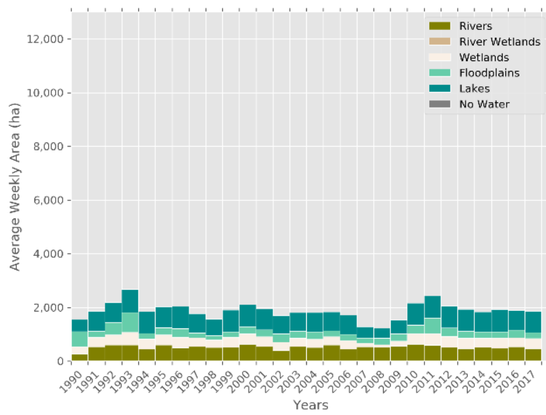
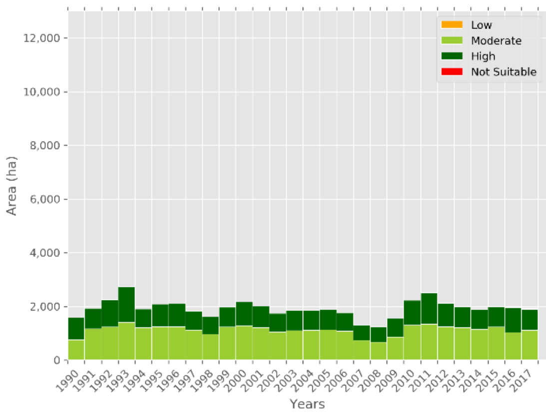
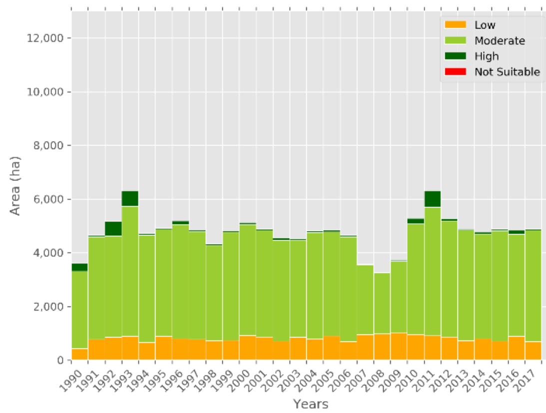
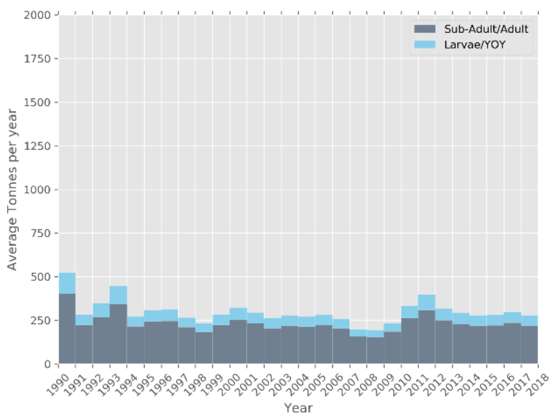
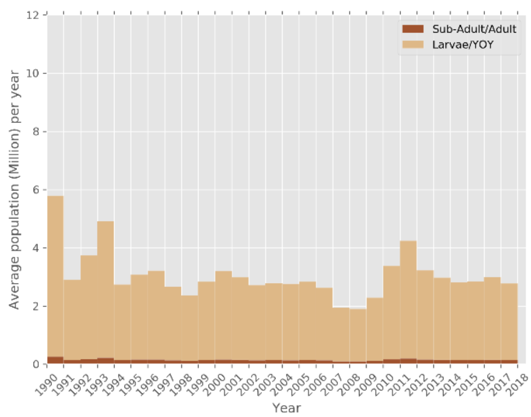


(d) Average annual biomass



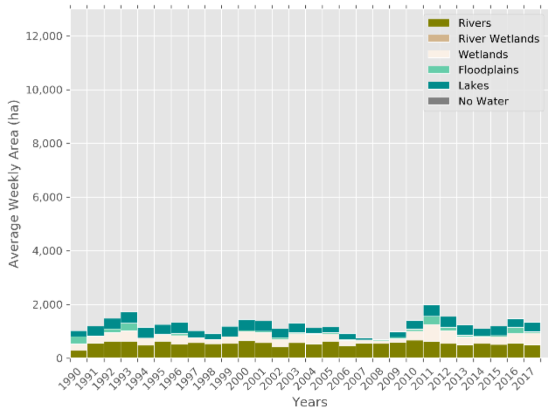
(e) Average annual population size



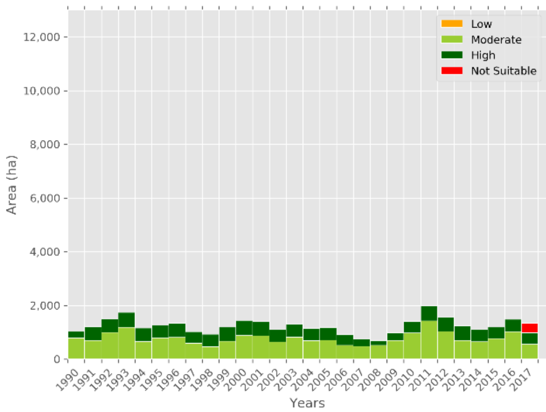
Zone 5 - Lock 5 to Lock 4	
	(a) Hydrological classes 
(b) Sub-adult/adult suitability 	(c) Larvae / YOY suitability 
(d) Average annual biomass 	(e) Average annual population size 

Zone 6 - Lock 6 to Lock 5

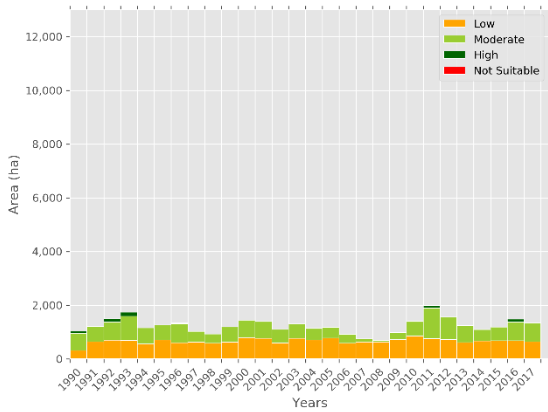
(a) Hydrological classes



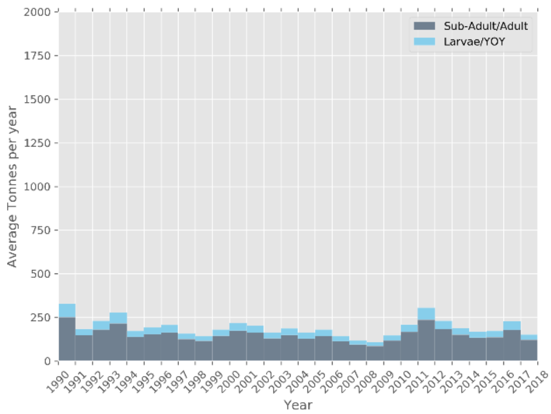
(b) Sub-adult/adult suitability



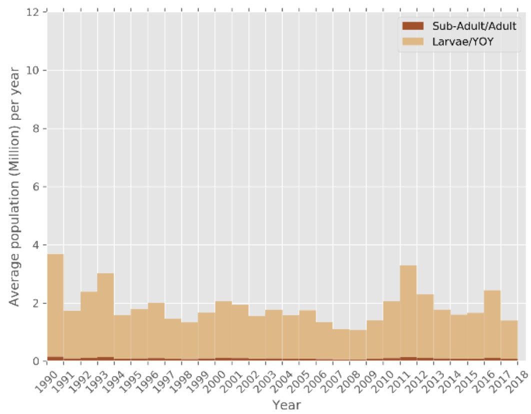
(c) Larvae / YOY suitability



(d) Average annual biomass

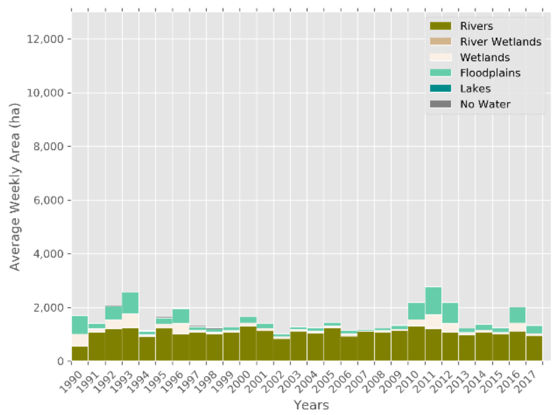


(e) Average annual population size

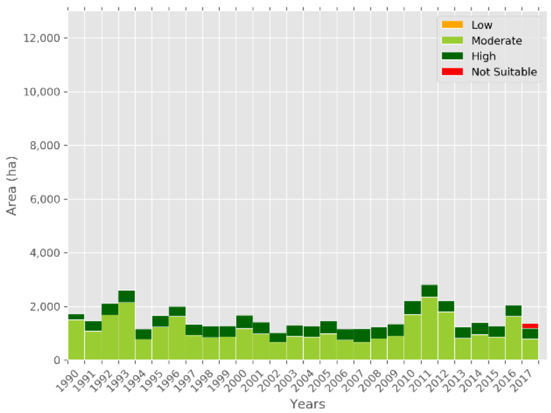


Zone 7 - Lock 7 to Lock 6 (Chowilla Reserve)

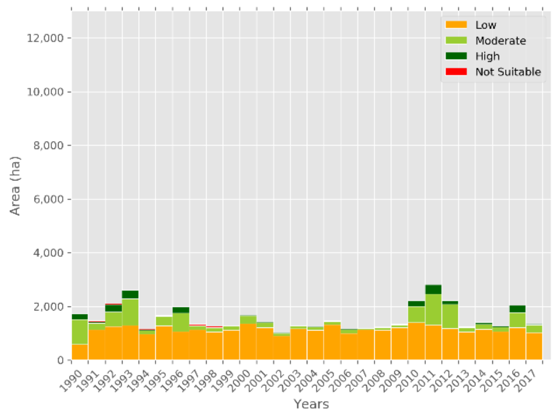
(a) Hydrological classes



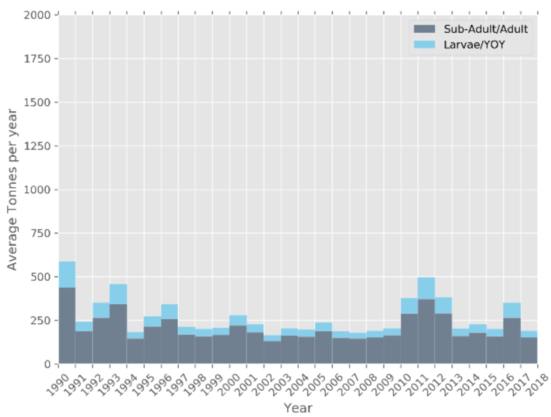
(b) Sub-adult/adult suitability



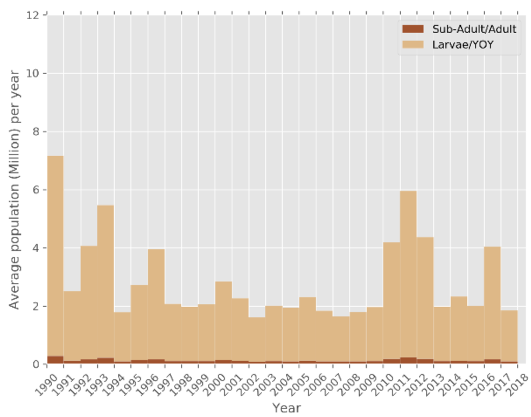
(c) Larvae / YOY suitability



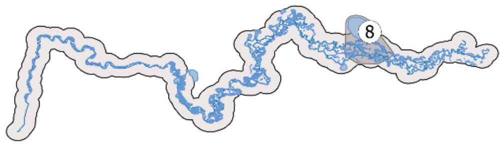
(d) Average annual biomass



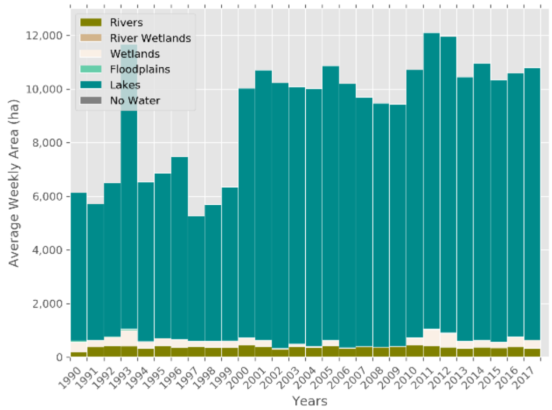
(e) Average annual population size



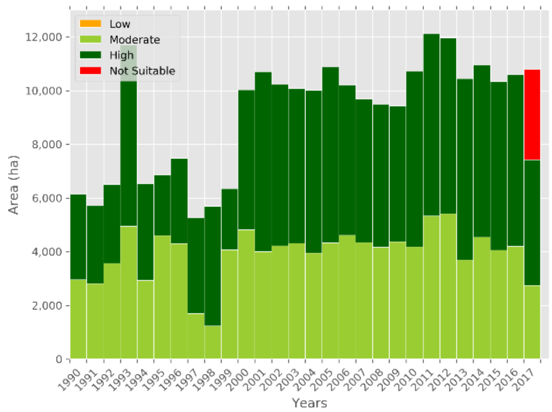
Zone 8 - Lock 8 to Lock 7 (Lake Victoria)



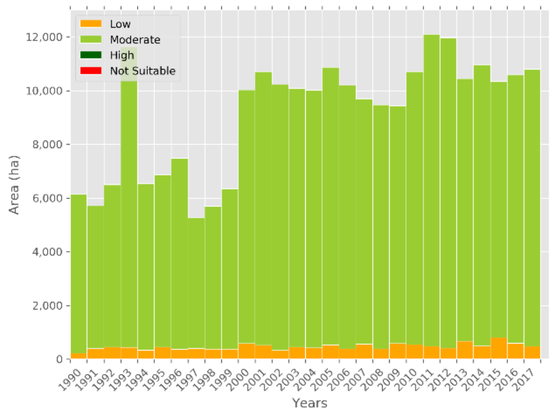
(a) Hydrological classes



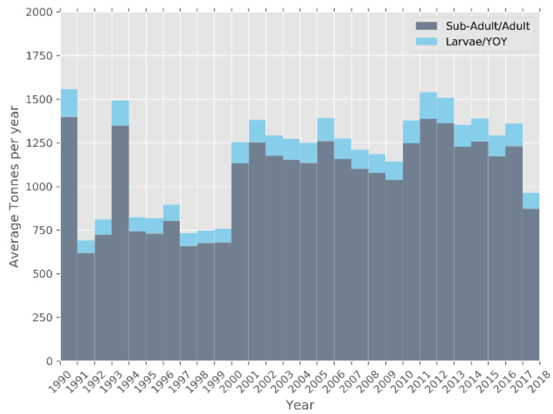
(b) Sub-adult/adult suitability



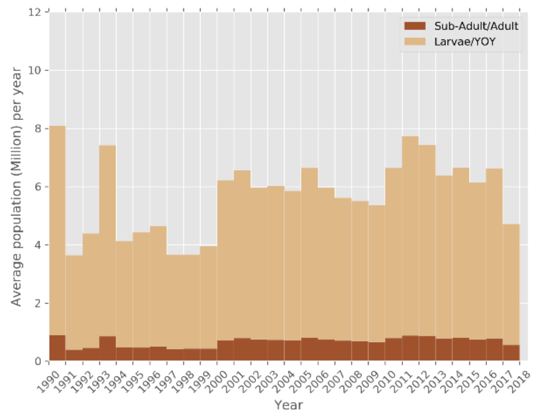
(c) Larvae / YOY suitability



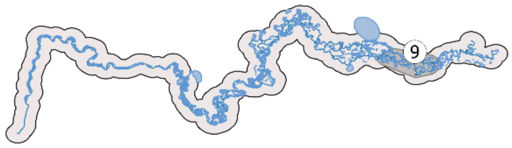
(d) Average annual biomass



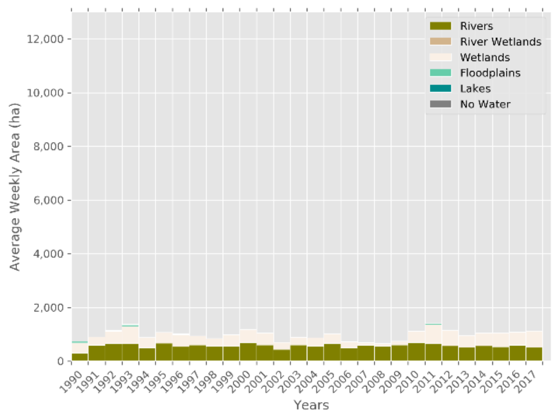
(e) Average annual population size



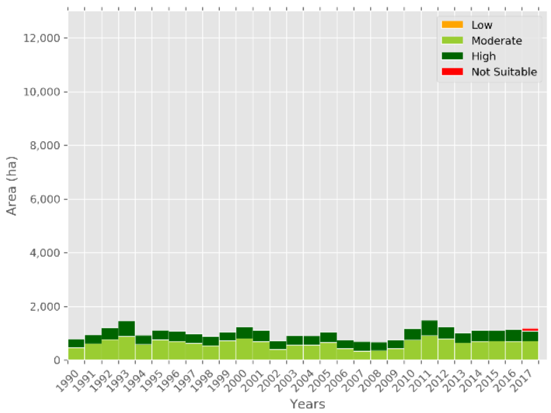
Zone 9 - Lock 9 to Lock 8



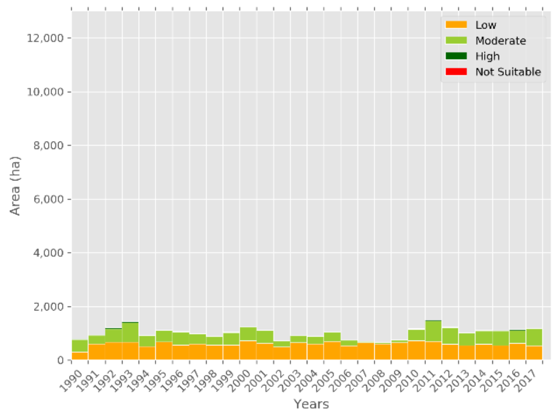
(a) Hydrological classes



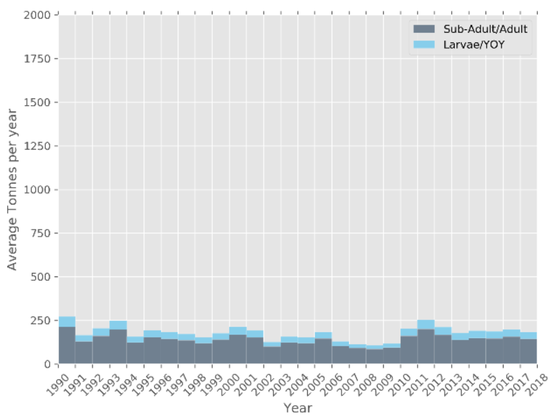
(b) Sub-adult/adult suitability



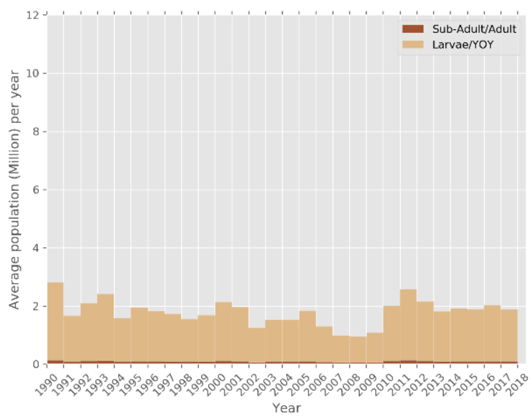
(c) Larvae / YOY suitability



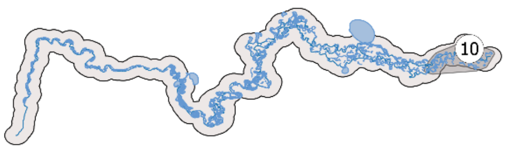
(d) Average annual biomass



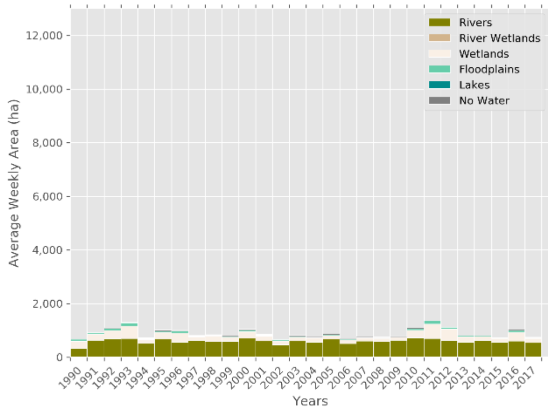
(e) Average annual population size



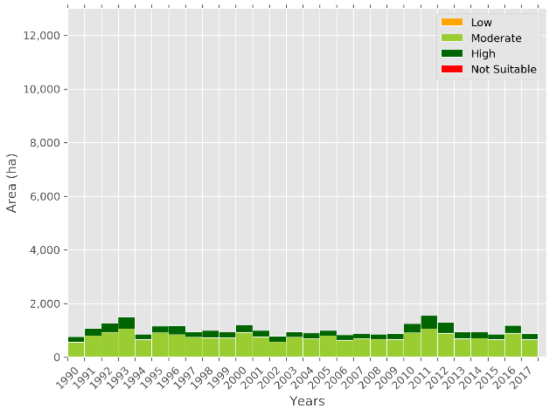
Zone 10 - Lock 10 - Lock 9



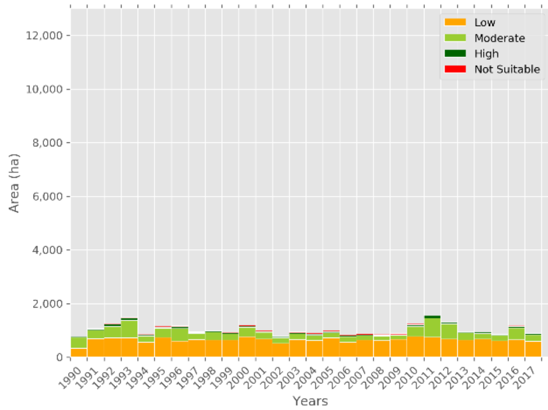
(a) Hydrological classes



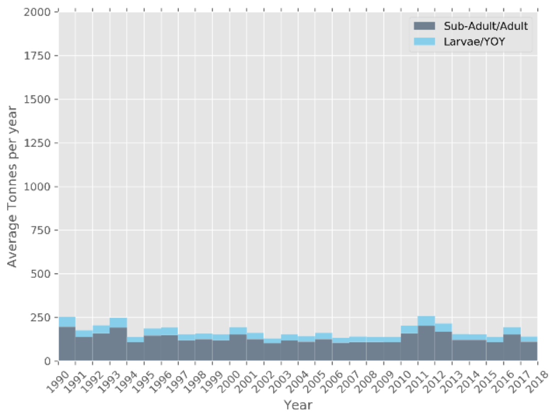
(b) Sub-adult/adult suitability



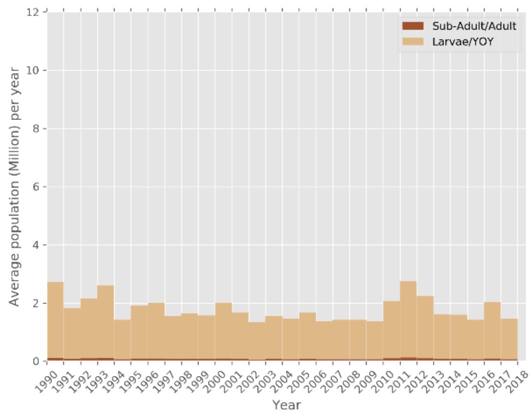
(c) Larvae / YOY suitability



(d) Average annual biomass

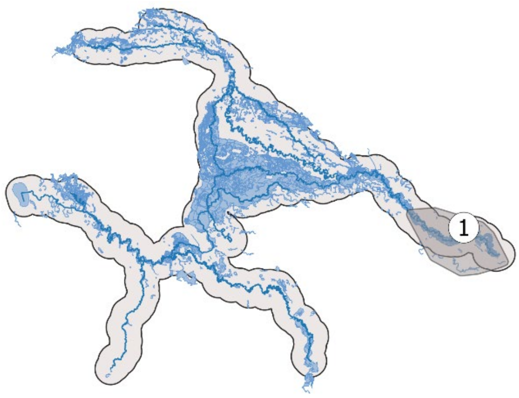


(e) Average annual population size

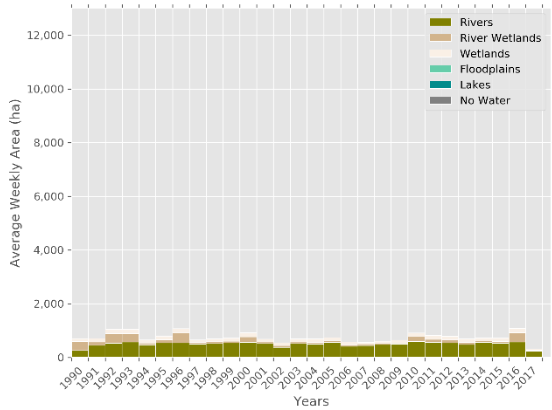


d. Mid-Murray River catchment

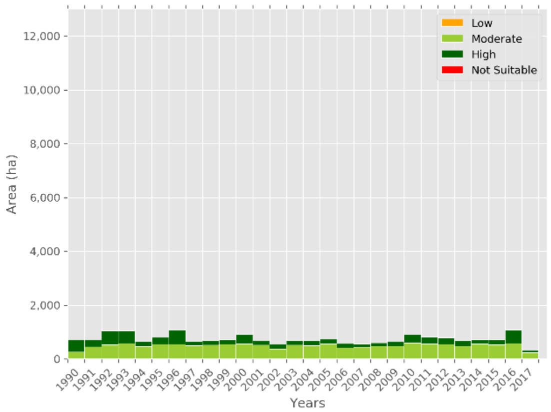
Zone 1 - Downstream of Yarrawonga Weir



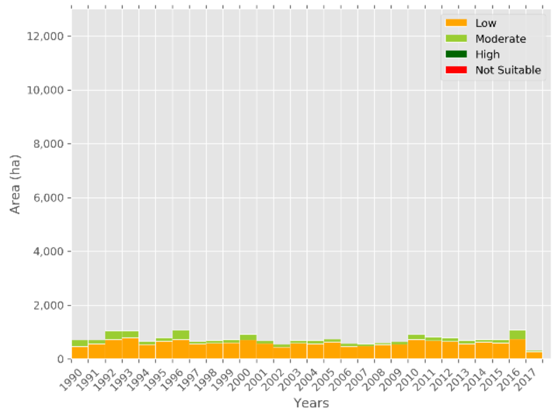
(a) Hydrological classes



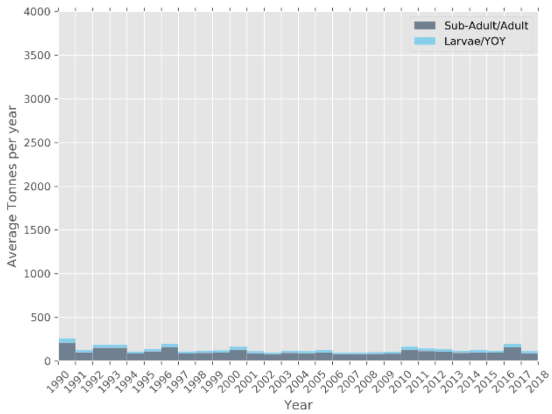
(b) Sub-adult/adult suitability



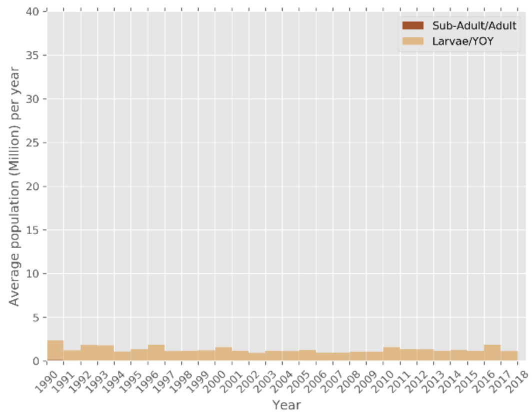
(c) Larvae / YOY suitability



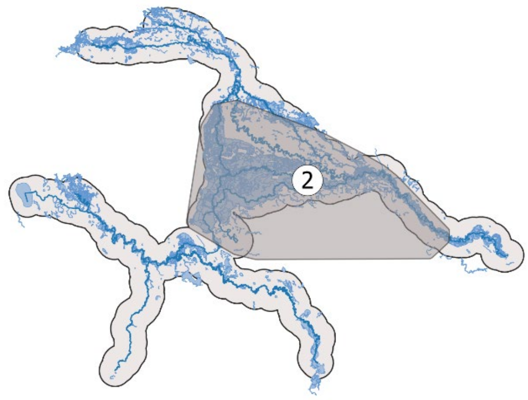
(d) Average annual biomass



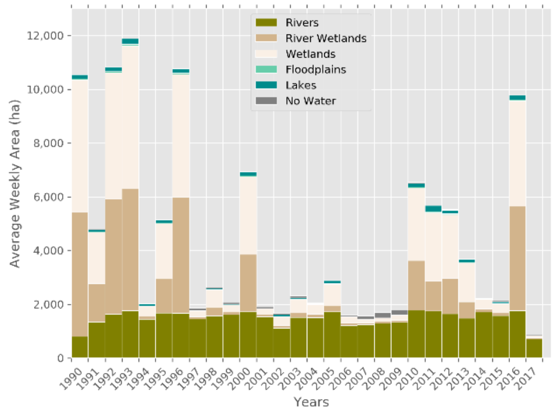
(e) Average annual population size



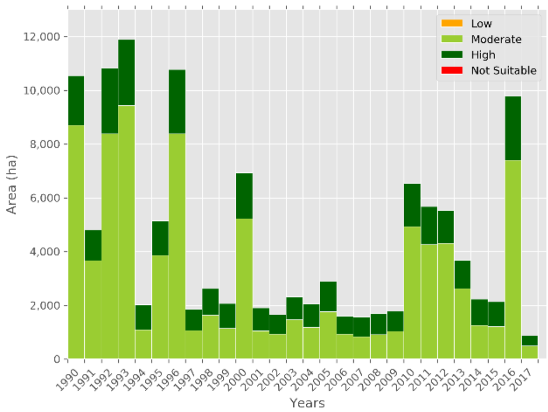
Zone 2 – Barmah-Millewa Forest



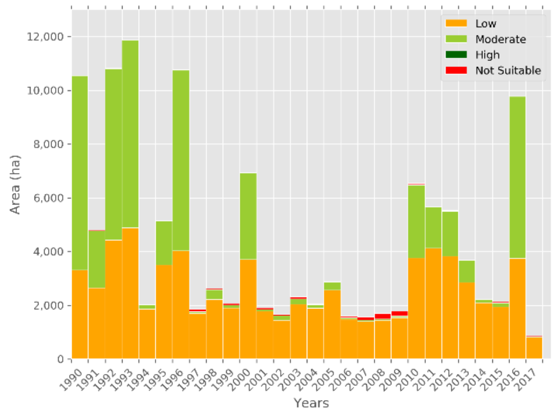
(a) Hydrological classes



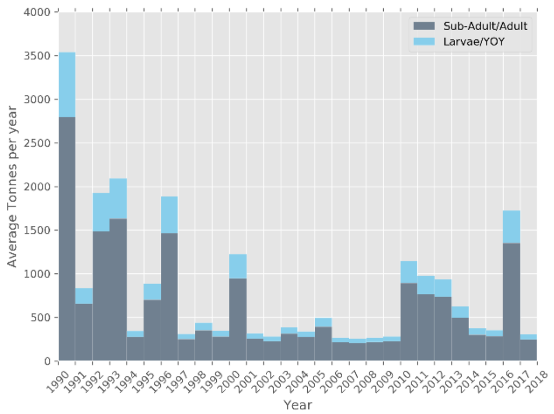
(b) Sub-adult/adult suitability



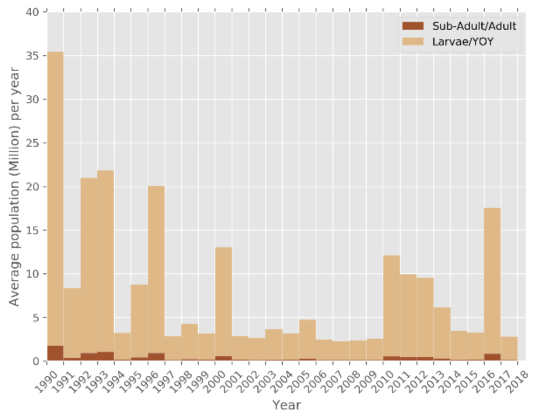
(c) Larvae / YOY suitability



(d) Average annual biomass



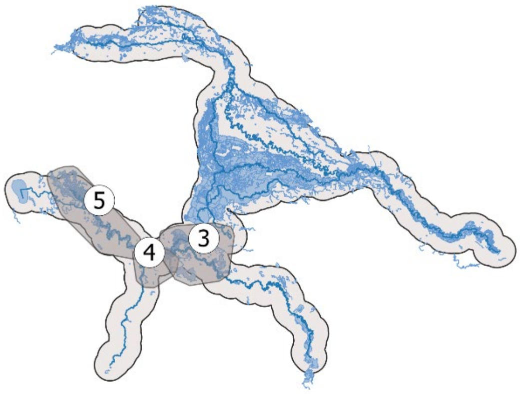
(e) Average annual population size



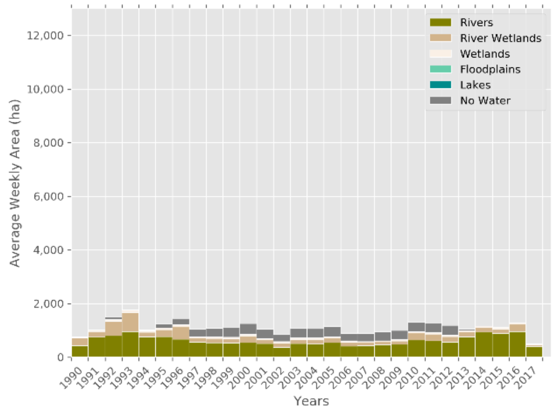
Zone 3 - Murray River - downstream of Barmah Choke

Zone 4 - Murray River - Between Goulburn River and Campaspe River

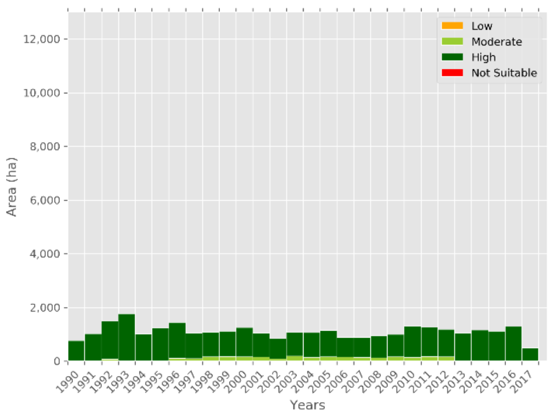
Zone 5 - Murray River - downstream of Campaspe River



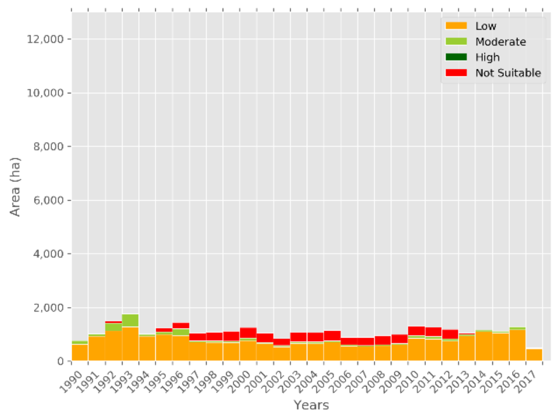
(a) Hydrological classes



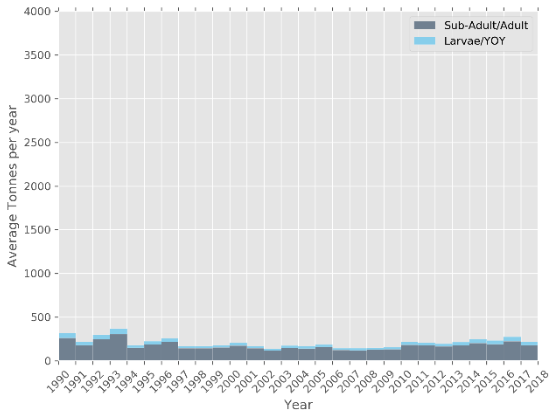
(b) Sub-adult/adult suitability



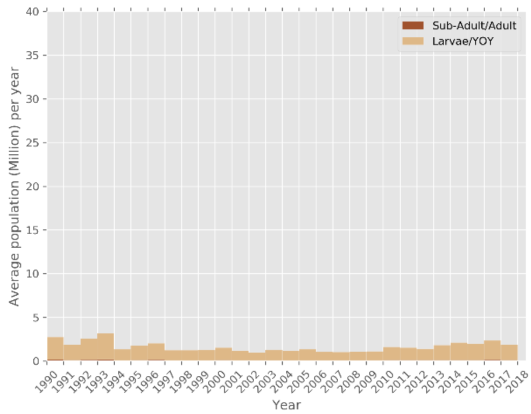
(c) Larvae / YOY suitability



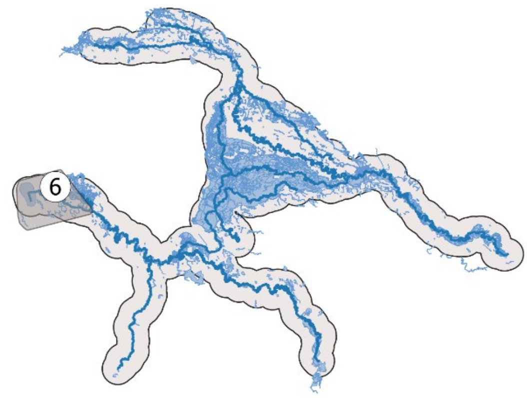
(d) Average annual biomass



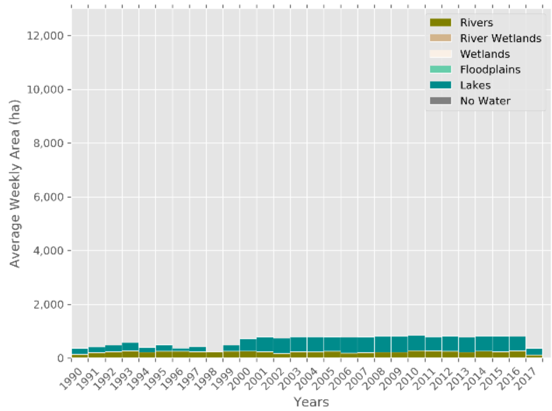
(d) Average annual population size



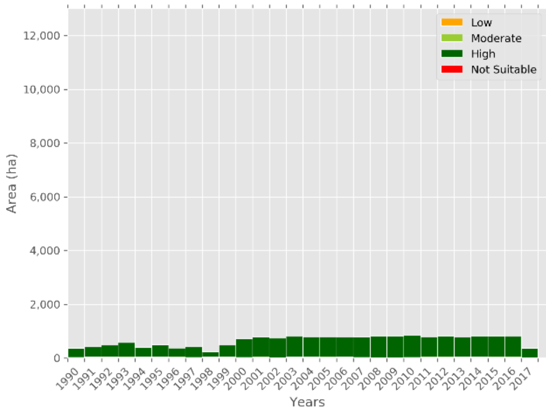
Zone 6 - Taylor Creek and Kow Swamp



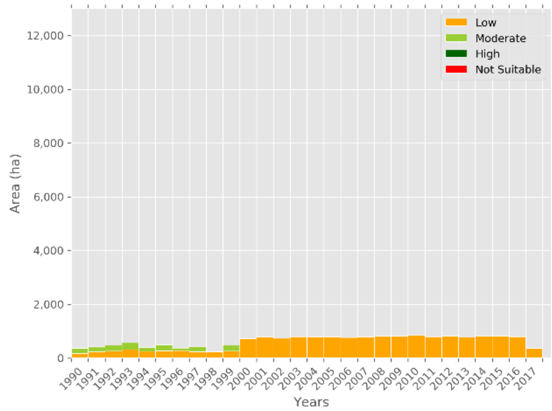
(a) Hydrological classes



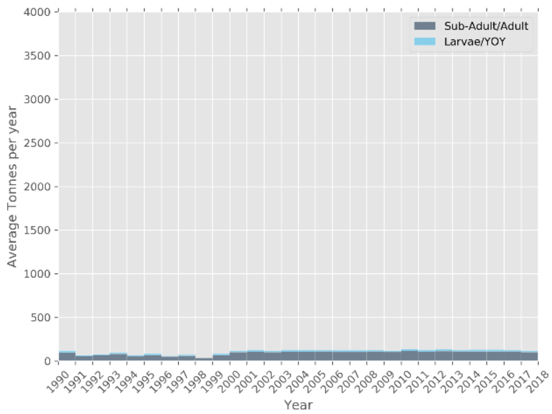
(b) Sub-adult/adult suitability



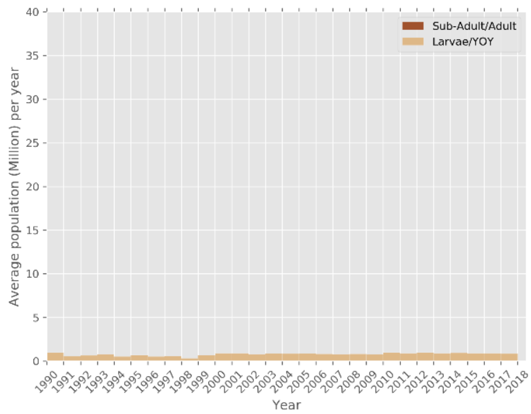
(c) Larvae / YOY suitability



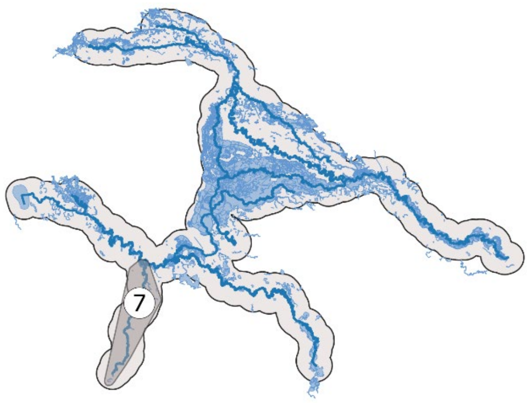
(d) Average annual biomass



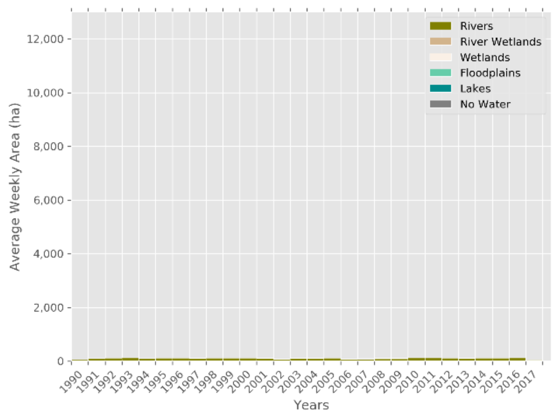
(e) Average annual population size



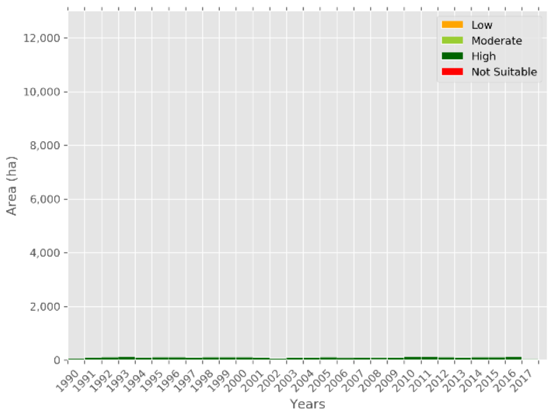
Zone 7 – Campaspe River



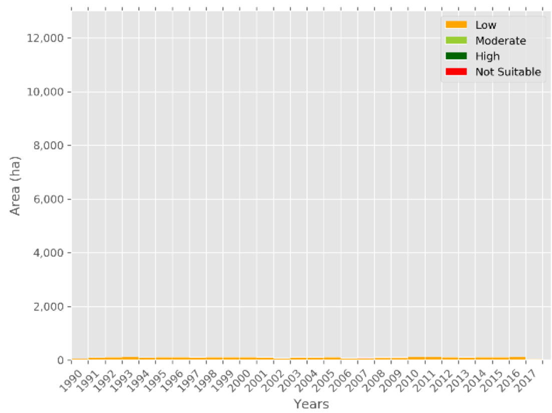
(a) Hydrological classes



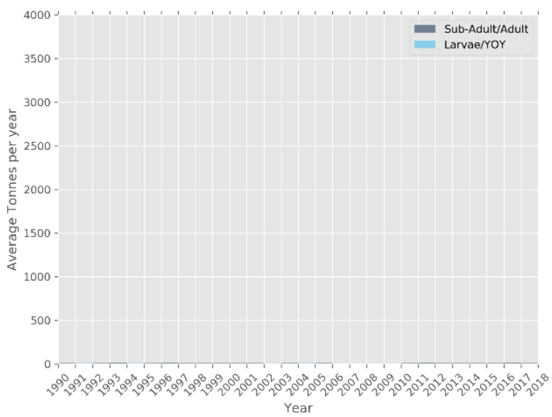
(b) Sub-adult/adult suitability



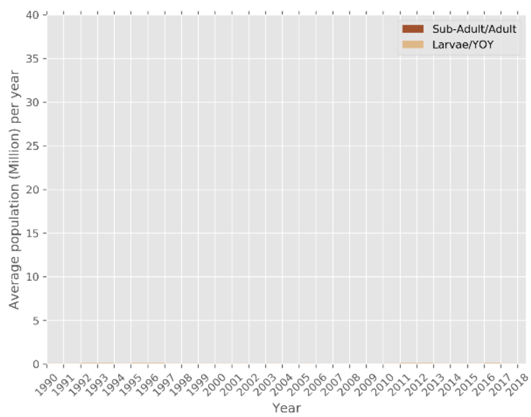
(c) Larvae / YOY suitability



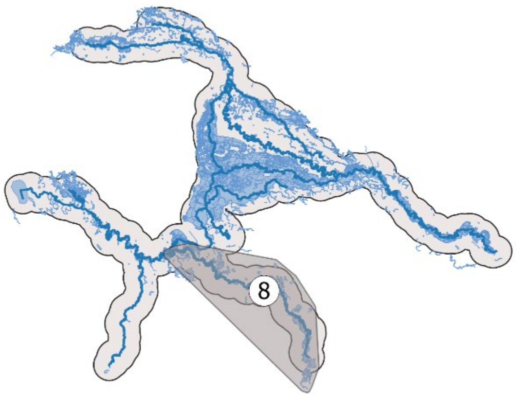
(d) Average annual biomass



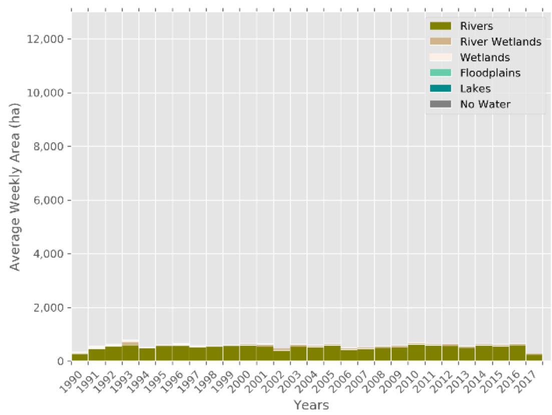
(e) Average annual population size



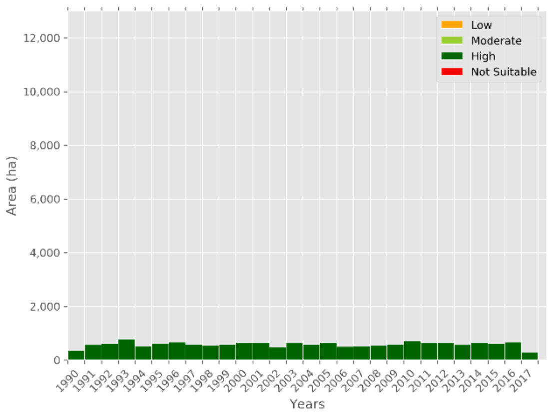
Zone 8 – Goulburn River



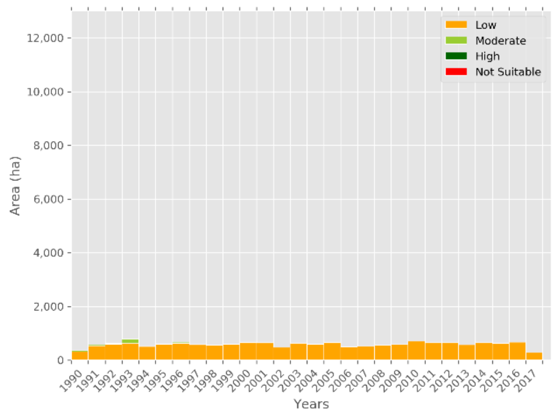
(a) Hydrological classes



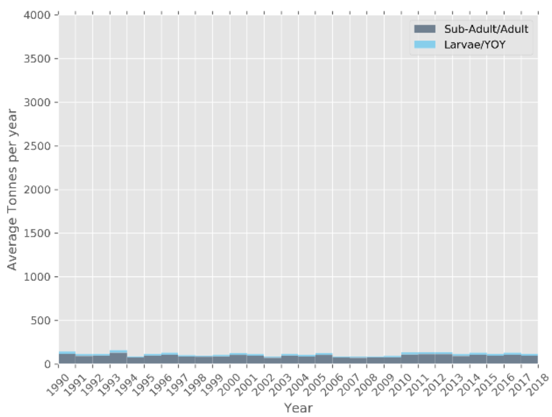
(b) Sub-adult/adult suitability



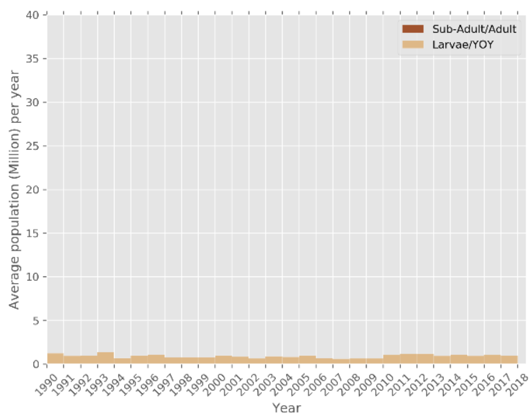
(c) Larvae / YOY suitability



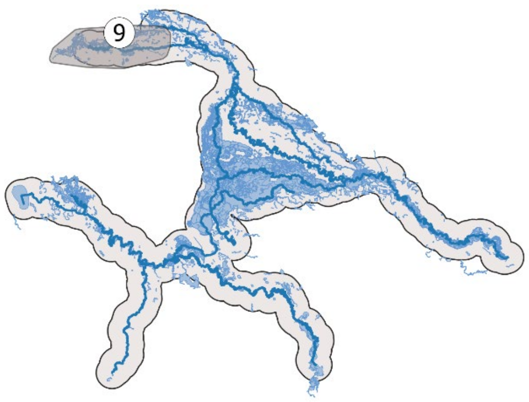
(d) Average annual biomass



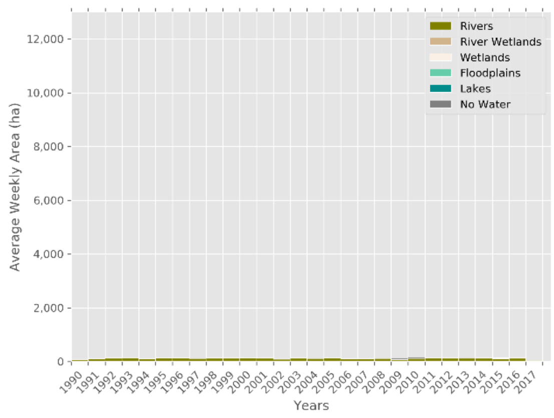
(e) Average annual population size



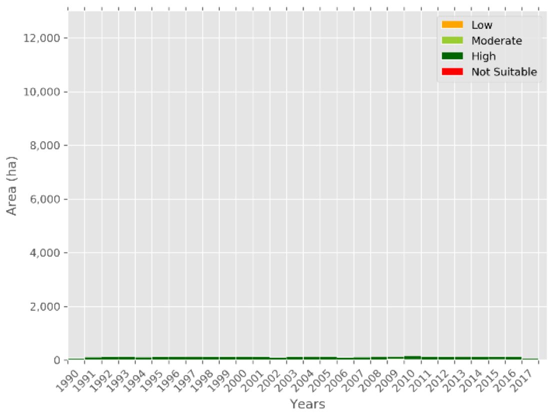
Zone 9- Wakool River



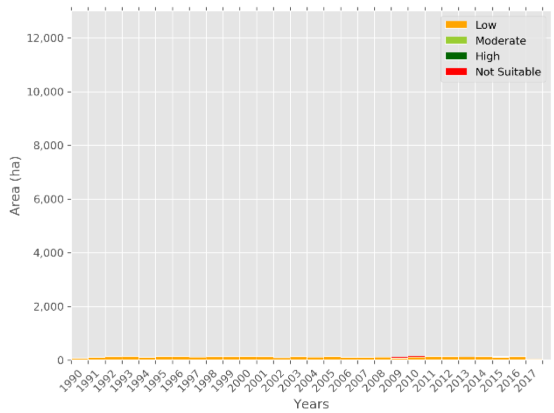
(a) Hydrological classes



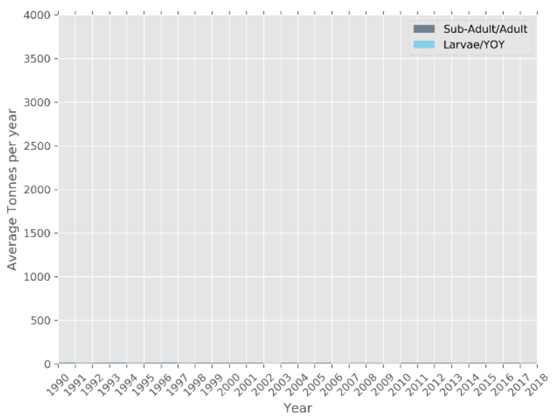
(b) Sub-adult/adult suitability



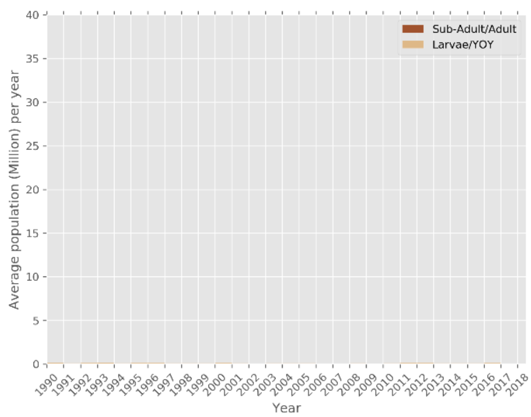
(c) Larvae / YOY suitability



(d) Average annual biomass

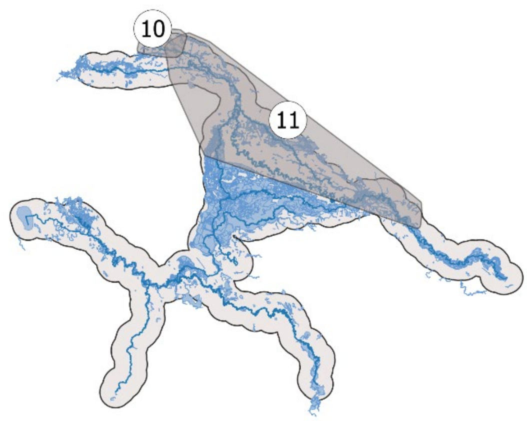


(e) Average annual population size

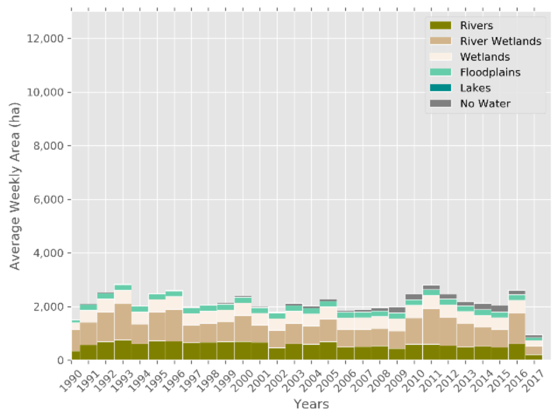


Zone 10 - Edward River

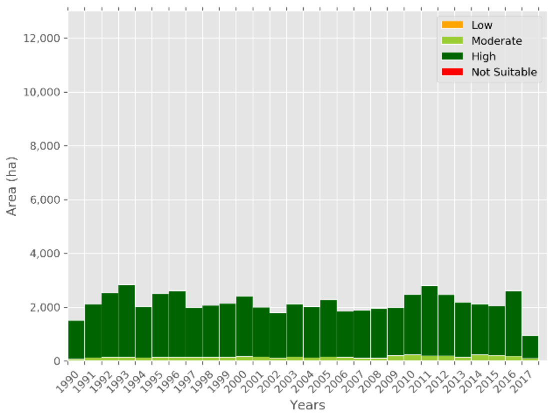
Zone 11 - Edward River, Tuppal Creek and Bullatale Creek - Wakool River



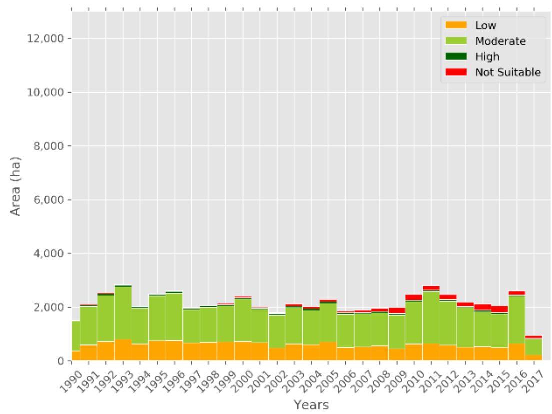
(a) Hydrological classes



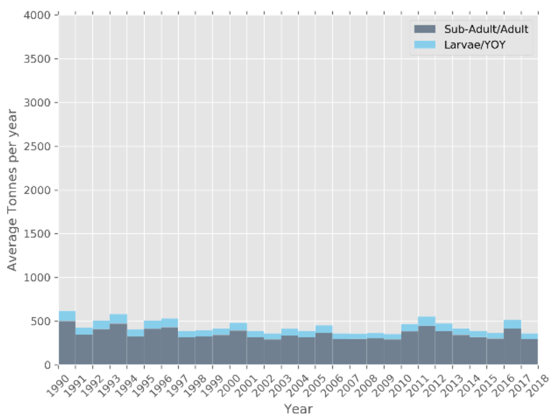
(b) Sub-adult/adult suitability



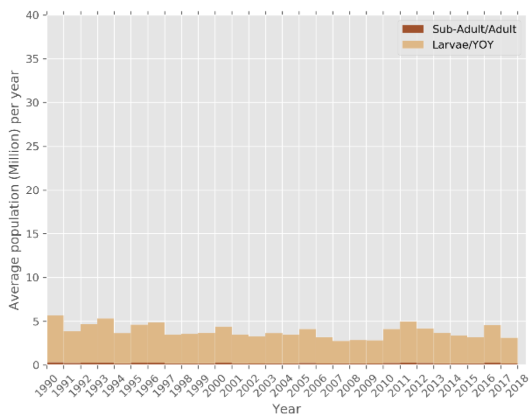
(c) Larvae / YOY suitability



(d) Average annual biomass

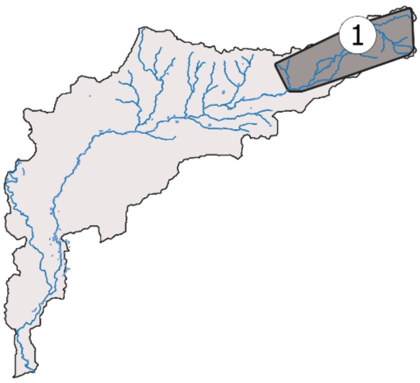


(e) Average annual population size

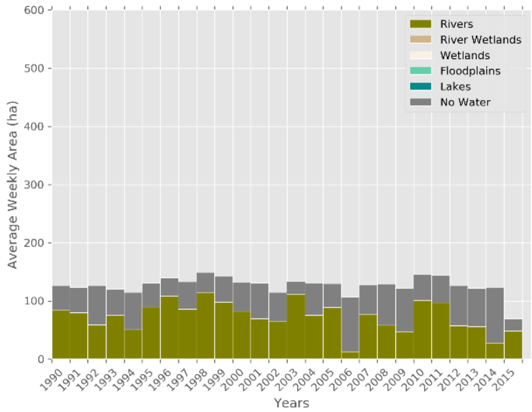


e. Moonie River catchment

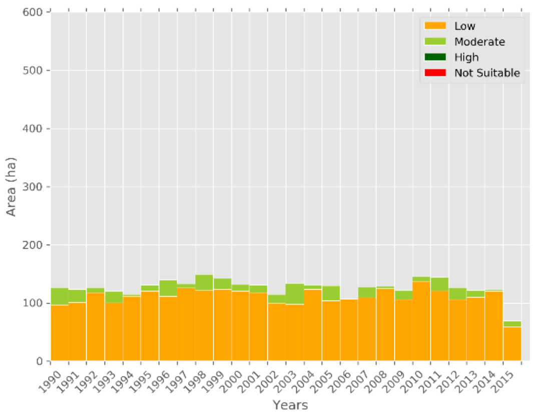
Zone 1 - (M1) Upstream of AMTD 345.0km ±. (below Moonie/Toombilla Ck junction)



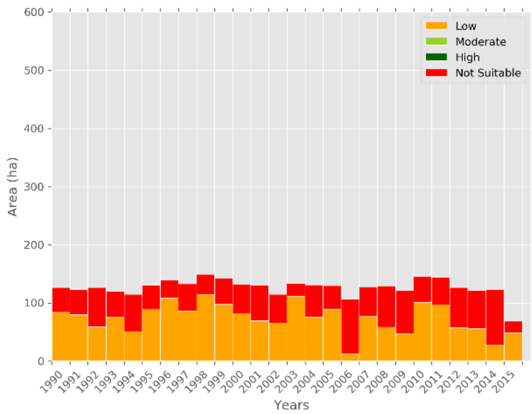
(a) Hydrological classes



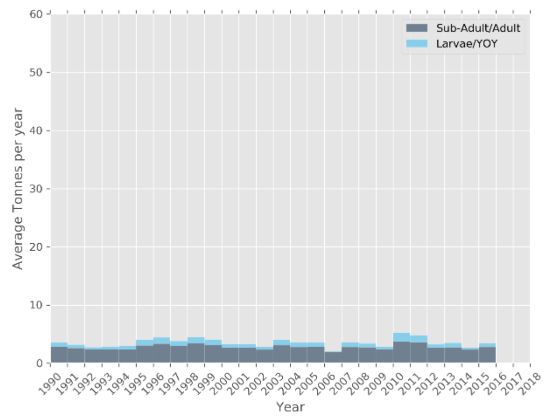
(b) Sub-adult/adult suitability



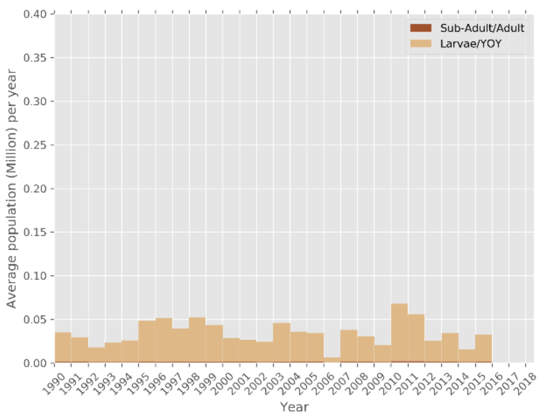
(c) Larvae / YOY suitability



(d) Average annual biomass

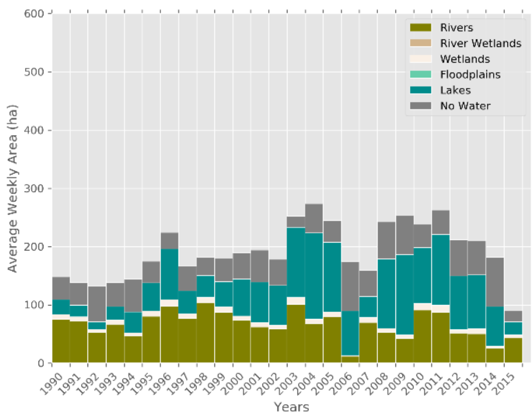


(e) Average annual population size

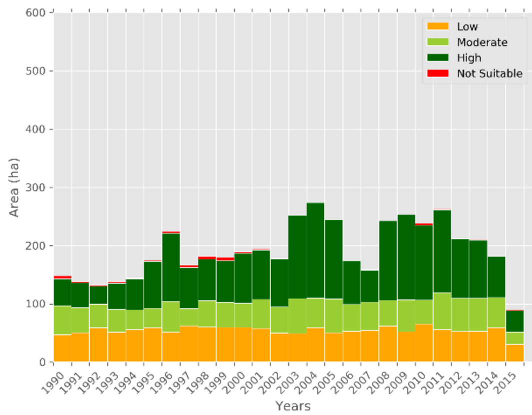


Zone 2 – (M2) Between AMTD 345.0km to AMTD 276.0km

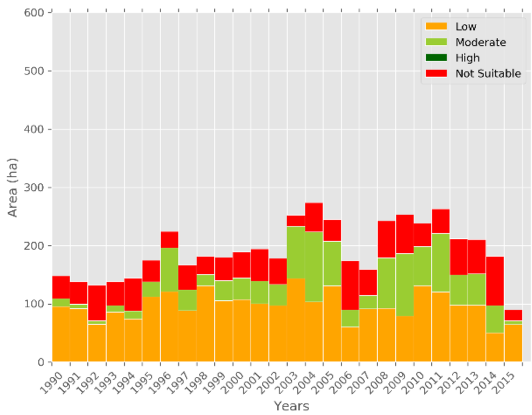
(a) Hydrological classes



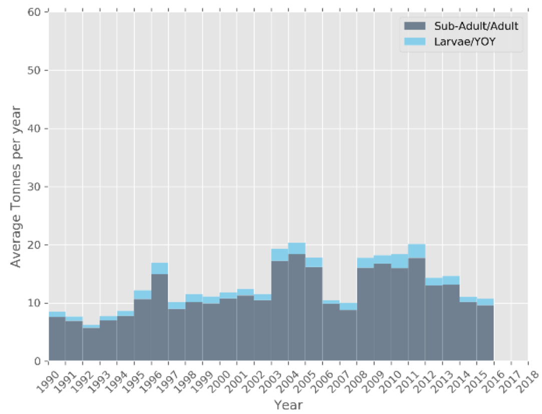
(b) Sub-adult/adult suitability



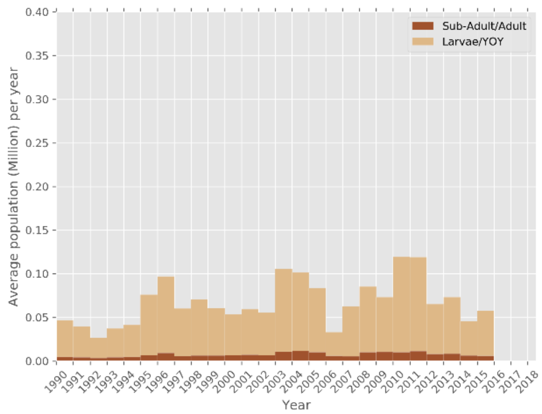
(c) Larvae / YOY suitability



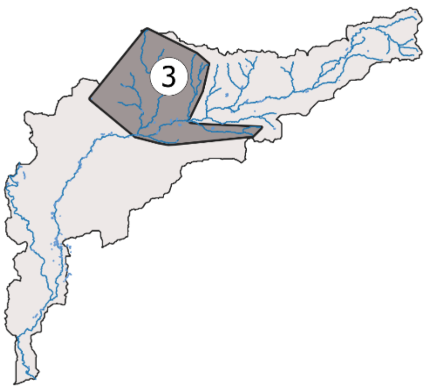
(d) Average annual biomass



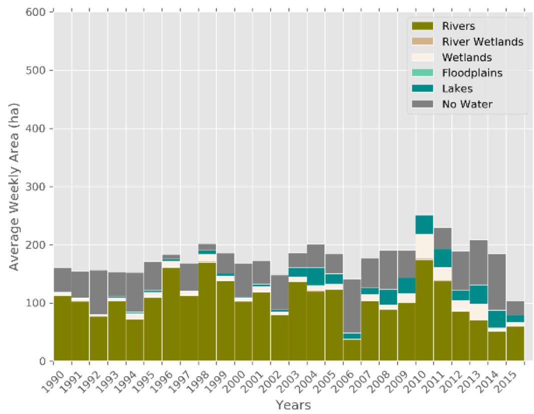
(e) Average annual population size



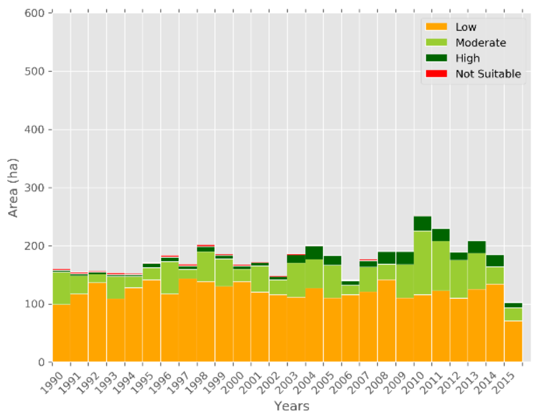
Zone 3 - (M3) Between AMTD 276.0km to AMTD 220.0km Approx



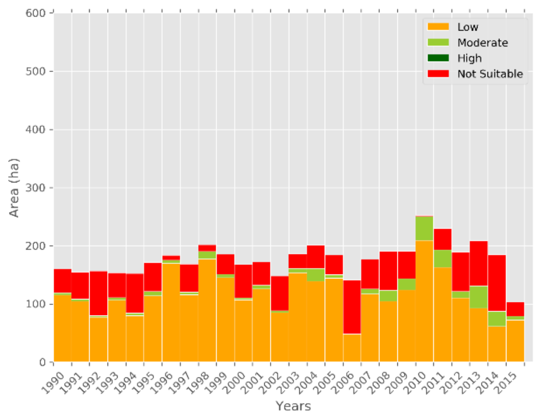
(a) Hydrological classes



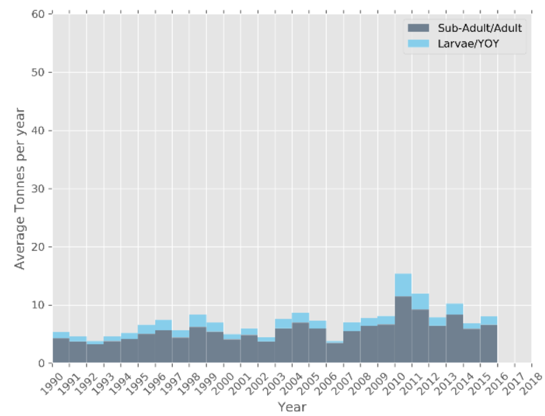
(b) Sub-adult/adult suitability



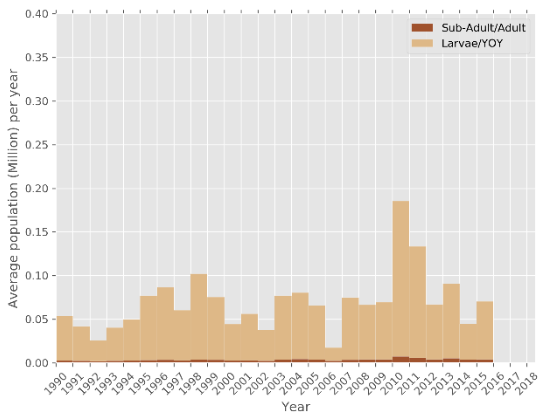
(c) Larvae / YOY suitability



(d) Average annual biomass

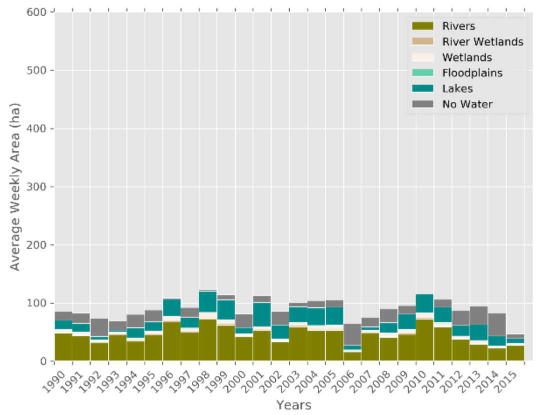


(e) Average annual population size

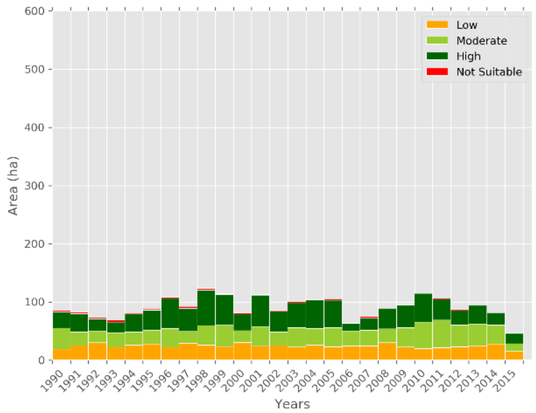


Zone 4 - (M4) Between AMTD 220.0km Approx to AMTD 168.0km (approx.)

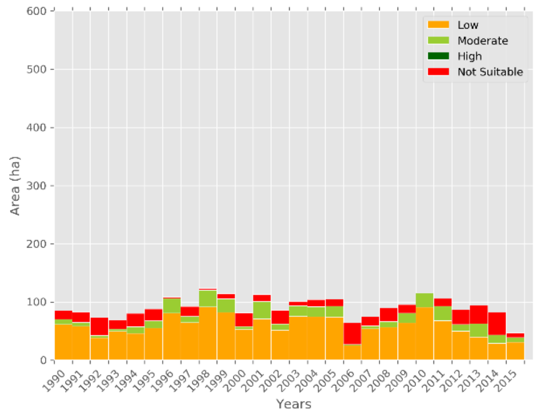
(a) Hydrological classes



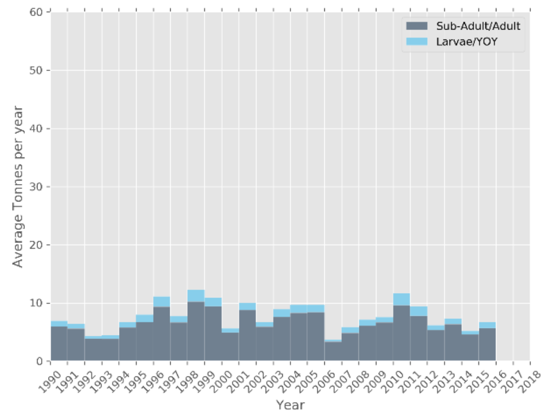
(b) Sub-adult/adult suitability



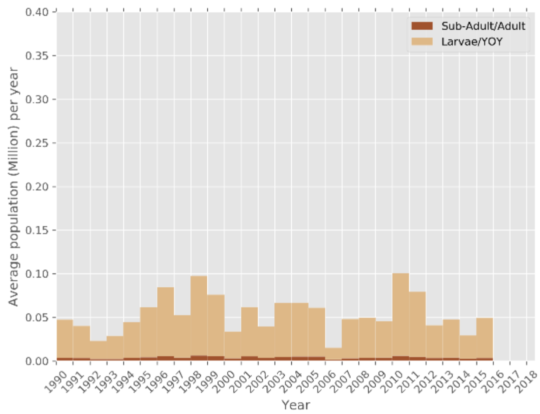
(c) Larvae / YOY suitability



(d) Average annual biomass

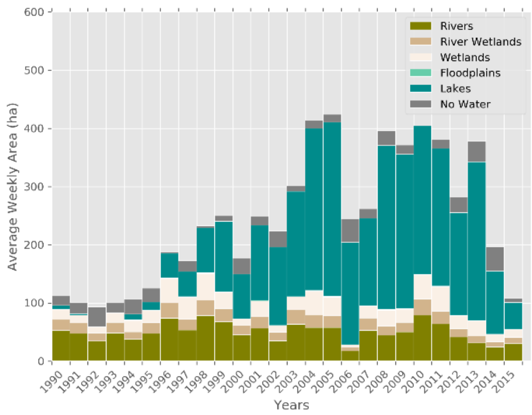


(e) Average annual population size

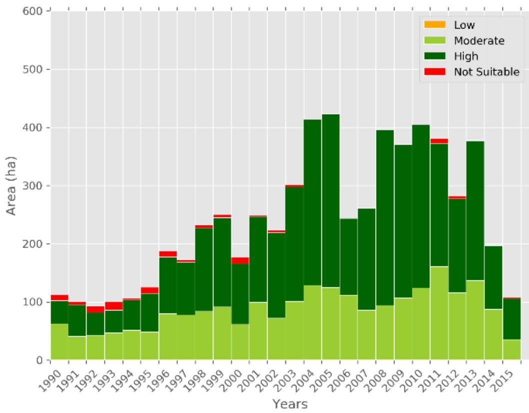


Zone 5 - (M5) Between AMTD 168.0 (approx.) to Nindigully Gauge (AMTD 95.0km)

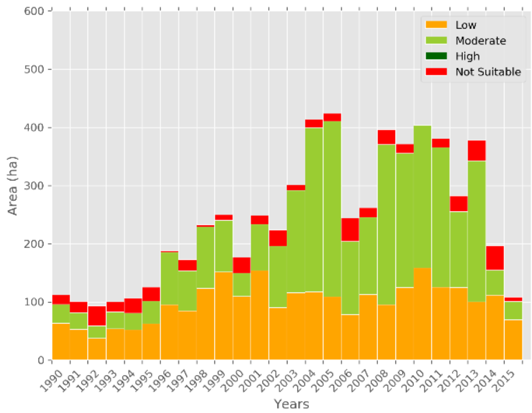
(a) Hydrological classes



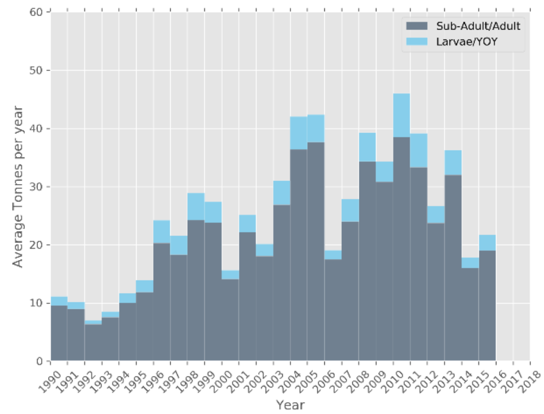
(b) Sub-adult/adult suitability



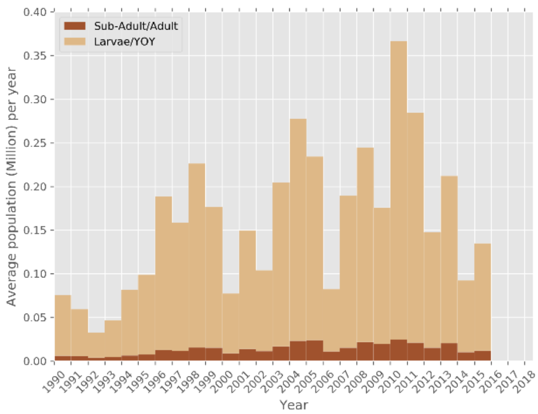
(c) Larvae / YOY suitability



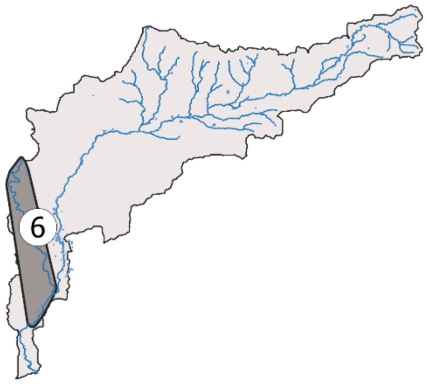
(d) Average annual biomass



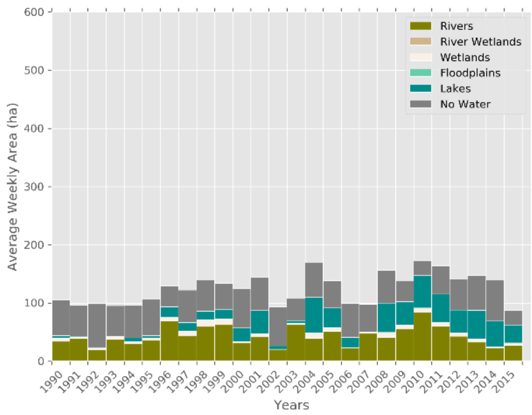
(e) Average annual population size



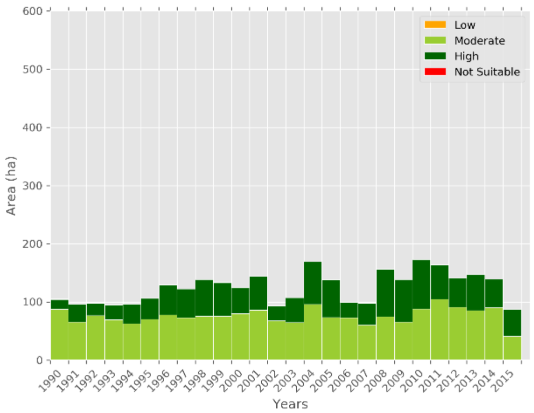
Zone 6 - (M6) Between Nindigully Gauge (AMTD 95.0km) to QLD/N.S.W. Border (Fenton)



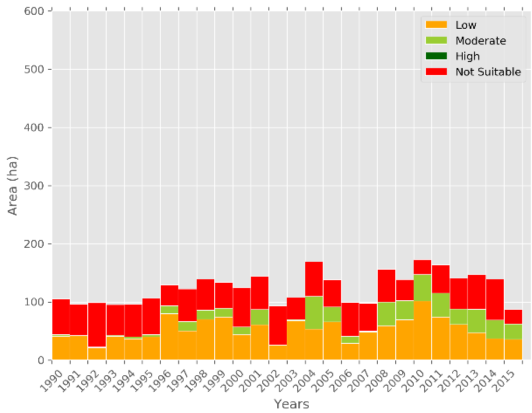
(a) Hydrological classes



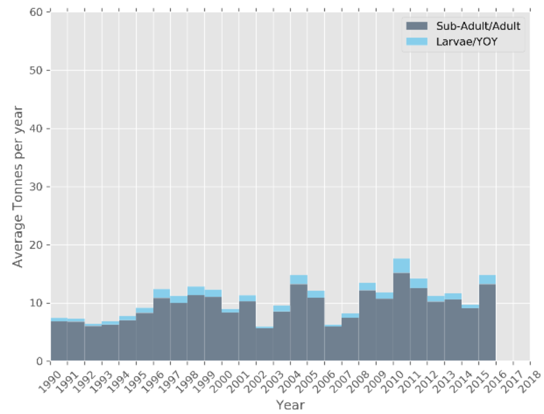
(b) Sub-adult/adult suitability



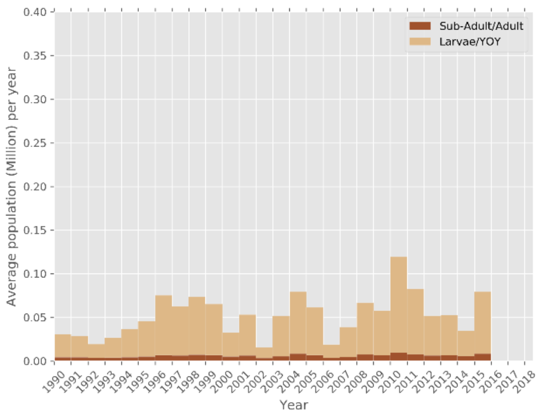
(c) Larvae / YOY suitability



(d) Average annual biomass

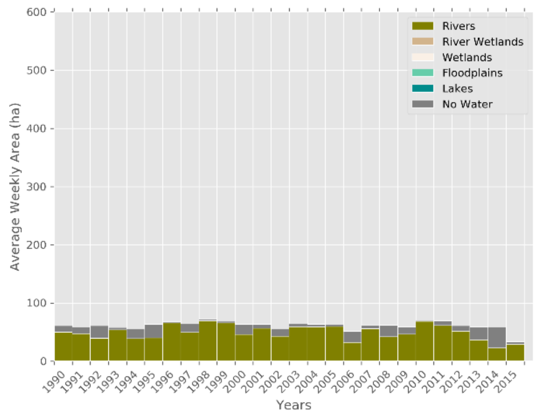


(e) Average annual population size

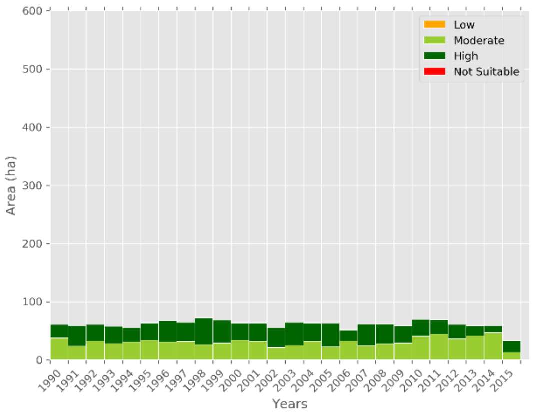


Zone 7 - (M7) QLD/N.S.W. Border (Fenton) to Moonie/Barwon Confluence

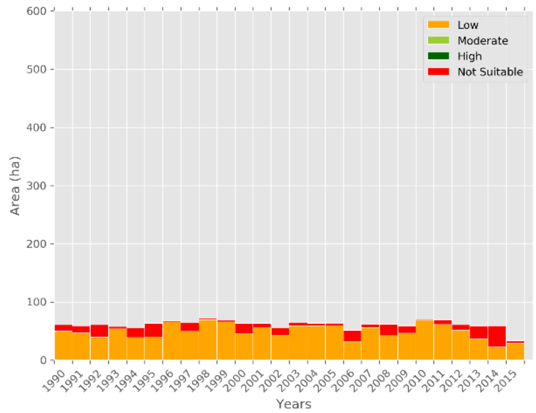
(a) Hydrological classes



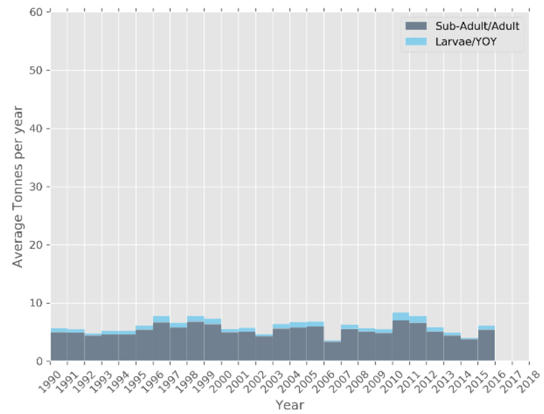
(b) Sub-adult/adult suitability



(c) Larvae / YOY suitability



(d) Average annual biomass



(e) Average annual population size

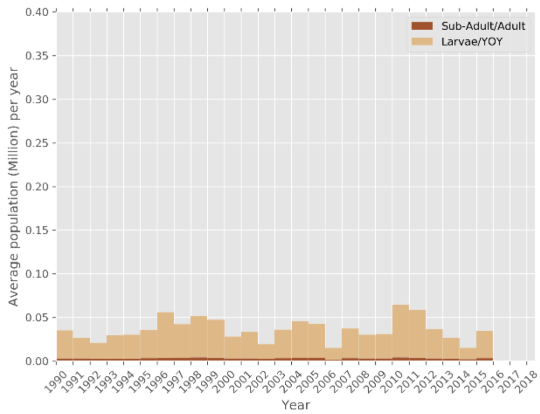
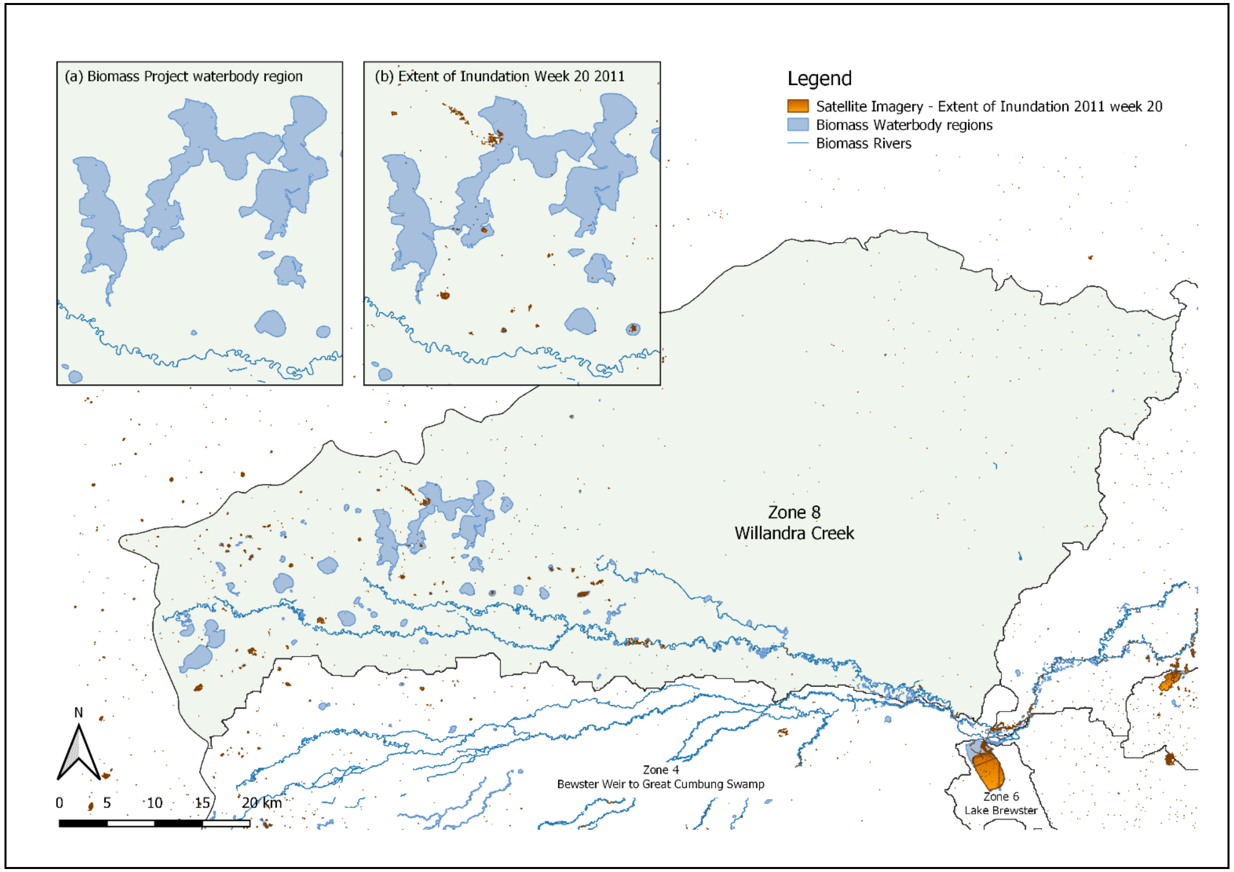


Figure S3

Case studies to test the hypothesis that the large variation between the NCCP Biomass Project and that derived from our habitat suitability estimates might be due to the former over-estimating the area of inundation. (a) Comparison of Zone 8 of the Lachlan River catchment as determined by satellite imagery for May 2011 in comparison to the maximum spatial extent of the Biomass Project dataset; and (b) Comparison of the area of inundation for Zone 2 of the Mid-Murray River catchment as determined by RiM-FIM imagery for May 2011 in comparison to the maximum spatial extent of the Biomass Project dataset

(a) Zone 8 Lachlan catchment



(b) Zone 2 Mid Murray catchment

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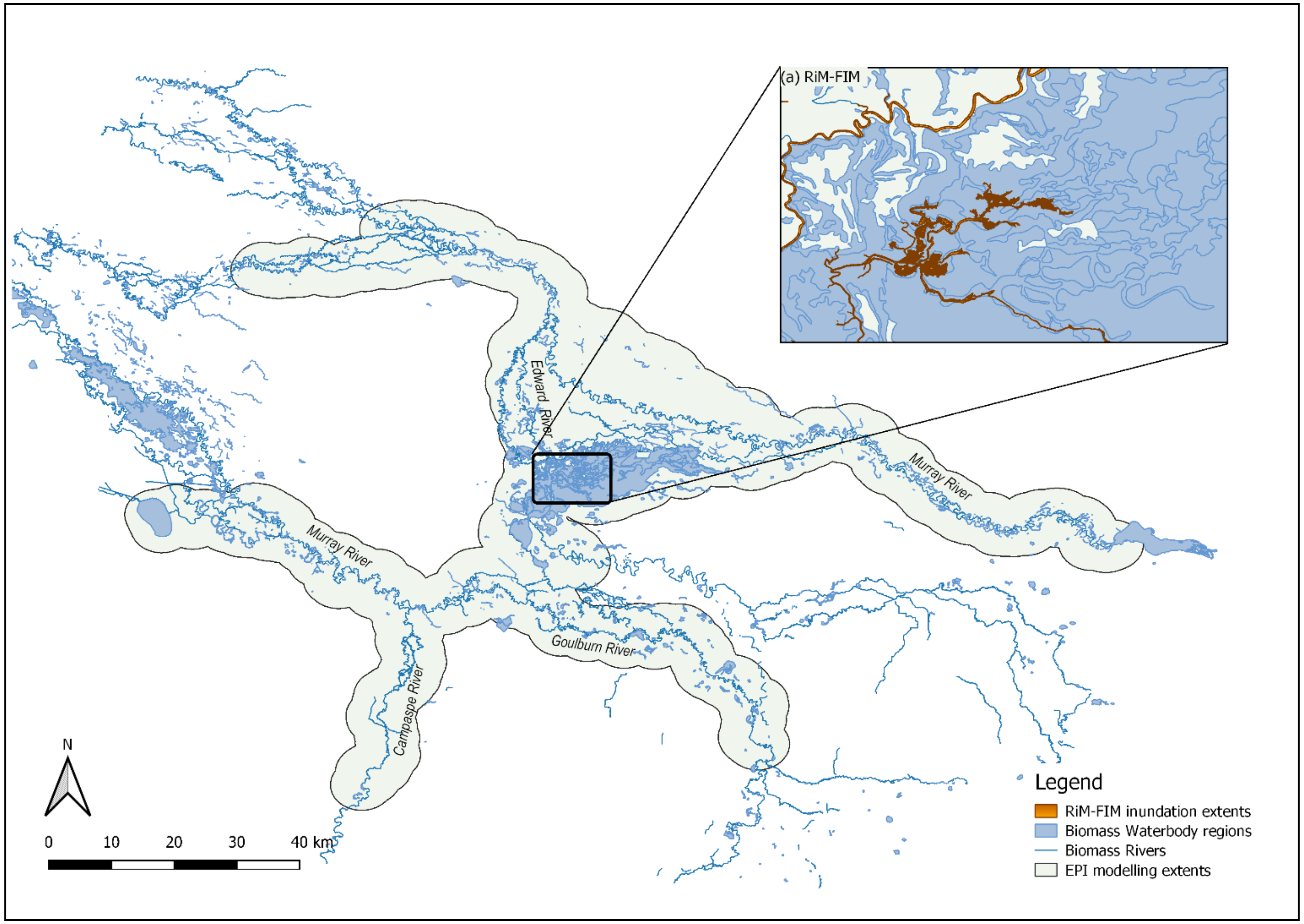
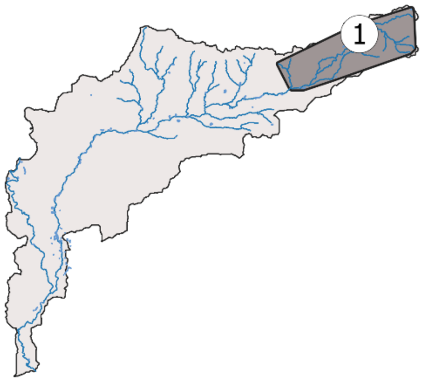
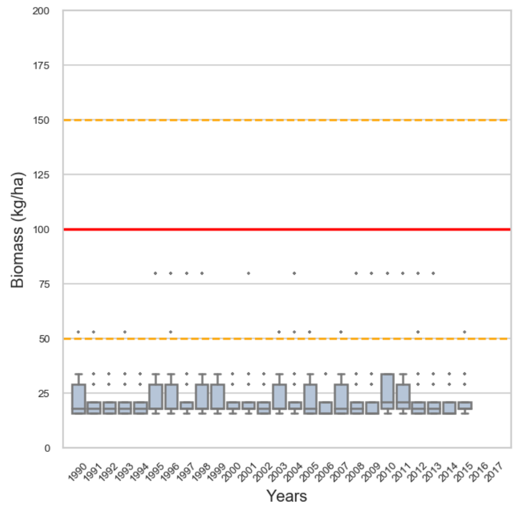


Figure S4

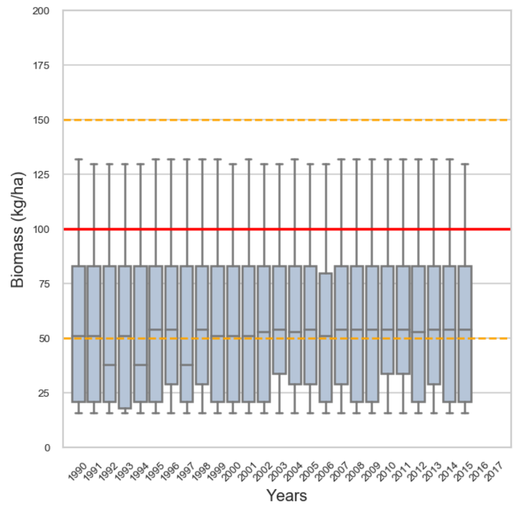
Time series of boxplots of the biomass density (kg/ha) for the Moonie catchment zones in relation to the three identified thresholds at which carp are hypothesised to induce ecological damage (50 kg/ha, 100 kg/ha and 150 kg/ha).

Zone 1

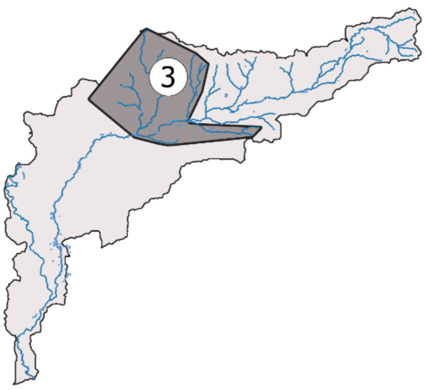


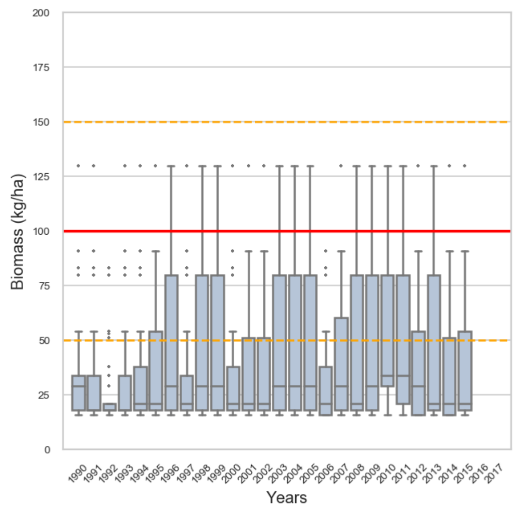


Zone 2

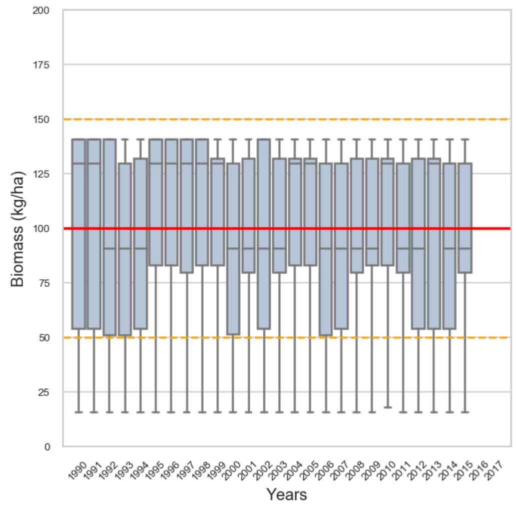


Zone 3

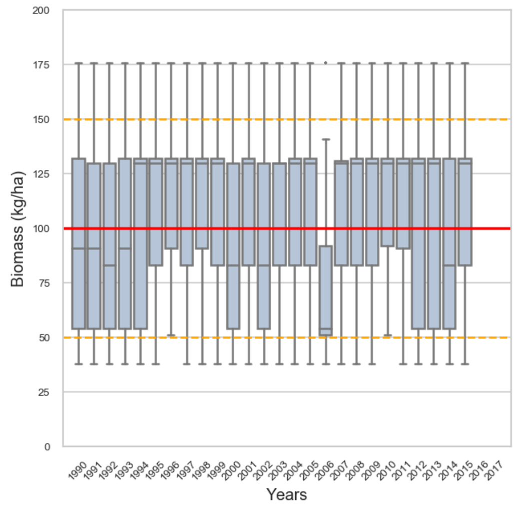




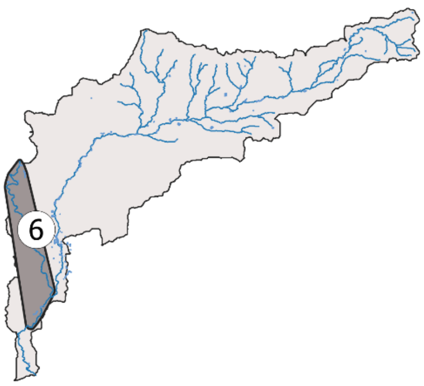
Zone 4

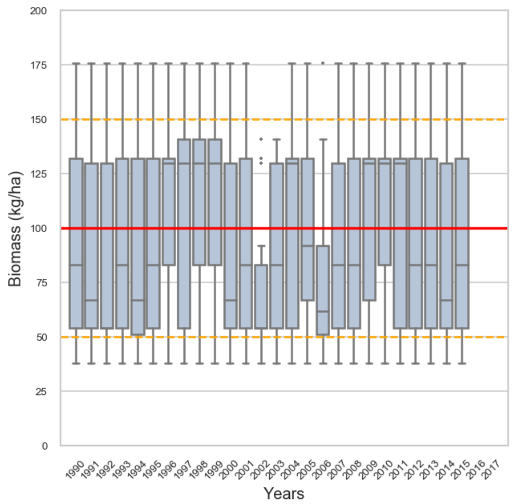


Zone 5



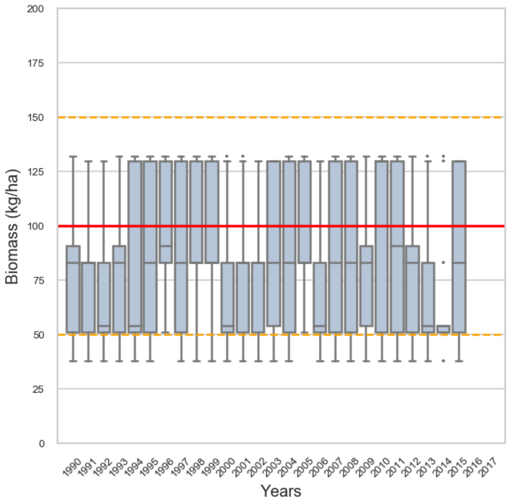
Zone 6





Zone 7


7


Biomass (kg/ha)
Years
0
25
50
75
100
125
150
175
200
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017

Supplementary tables

Table S1.

Key environmental variables and the spatial data (and manipulations) used as their proxies. BBN Abbreviations: YOY-L = Young of year / Larvae; A-SA = Adult / sub-adults. All data was imported to the project PostgreSQL database for further use.

KEV	BBN	Dynamic / static	Source data	Data manipulations
Adult Connectivity	YOY-L	Time Series	Downstream flow	A Python script was created to review the connectivity of the reach/water body for the post/previous week. If the discharge is over the drown out volumes for weirs available, then the spatial unit was deemed connected.
Dissolved Oxygen	YOY-L / A-SA	Time Series	DELWP Water Measurement Information System http://data.water.vic.gov.au/static.htm	Glenelg Data was downloaded from the DELWP monitoring website for the gauges located within the Glenelg catchment. Of 12,730 available records 0.32% were allocated a state of "Poor" whilst 22.93% were "Moderate" and 76.74% were defined as "Good". Where values were missing a state of "Good" was applied.
			A dataset was extracted from the FFRD 2 October 2014 (excel spreadsheet) by NSW DPI which included DO values.	Lachlan - The dates ranged from 17-06-1992 to 27-05-2014 and included 2103 records where only 1915 records had a valid reading for DO. Only 7.41% of the recorded dissolved oxygen was in a state of “Poor” whilst 41.94% was “Moderate” and 50.65% was defined as “Good”. Where data was available it was assigned the appropriate habitat state, where no data existed a state of “Moderate” was assigned.

KEV	BBN	Dynamic / static	Source data	Data manipulations
			Water Connect SA https://www.waterconnect.sa.gov.au/Systems/RTWD/Pages/Default.aspx	Lower Murray Data was downloaded from the SA Water Connect website and imported into the database. Of 18,137 available records 1.5% were allocated a state of "Poor" whilst 5.51% were "Moderate" and 92.99% were defined as "Good". Where values were missing a state of "Good" was applied.
			Water NSW https://realtimedata.waternsw.com.au/	Mid Murray Data was downloaded from the WaterNSW website and imported into the database. Of 12,051 available records 1.4% were allocated a state of "Poor" whilst 33.28% were "Moderate" and 65.31% were defined as "Good". Where values were missing a state of "Good" was applied.
				Moonie No recorded data was available for the time period. A suitability state of "Good" was allocated.
Downstream flow	A-SA	Time Series	Australian Bureau of Meteorology http://www.bom.gov.au/water/hrs/index.shtml	Where recorded gauge data was available from the Bureau of Meteorology online data warehouse, a python script was created to extract daily data using the Kiwis Pie python library. (https://github.com/amacd31/kiwis_pie) Where data was not available then flow records were assigned based on the modelling undertaken by Joehnk et al (2020) (Section 4.0 Water Temperature Modelling) For waterbodies downstream flow was allocated based on the recorded inundation and the waterbody type.

KEV	BBN	Dynamic / static	Source data	Data manipulations
Inundation	YOY-L	Time Series	MODIS Weekly >10% OWL (1.1. Hydrological and Inundation modelling) Landsat WOFS data - THREDDS Catalogue (https://www.ga.gov.au/scientific-topics/community-safety/flood/wofs)	This dataset was created by a bespoke Python script that calculated the area of intersecting MODIS or Landsat pixels to the waterbody geometry. For weeks where there were missing records due to the timing of the MODIS or Landsat data availability, an analysis was undertaken reviewing the prior 2 weeks and the future 2 weeks and then allocated values based on presence/absence for that extended time period.See Appendix 1.1.3. Inundation modelling
Location	YOY-L	Static	NSW Wetlands(2006) Australian National Aquatic Ecosystem (ANAE) Wetlands (Revision 2017) (https://data.gov.au/dataset/ds-dga-fe003aaa-09e5-41b7-9689-80c32d5fa1ac/details) VicMap hydro (https://discover.data.vic.gov.au/dataset/vicmap-hydro-1-25-000)	Simple definition of river or water body. Water bodies were sourced from the NSW Wetlands (2006), the Australian National Aquatic Ecosystem (ANAE) Wetlands or VicMap Hydro depending on the case study location.

KEV	BBN	Dynamic / static	Source data	Data manipulations
Photoperiod	YOY-L	Time Series		A python script using the ephem package (https://pypi.python.org/pypi/pyephem/) was written to create a database table holding the values of sunrise, noon and sunset for each day between the case study time-series dates. The photoperiod was a simple calculation of sunset - sunrise to give the total daylight hours. Glenelg - Casterton, latitude -37.58528, longitude 141.40377, elevation 51.3 m Lachlan - Lake Cargelligo, latitude -33.2427, longitude 146.4058, elevation 168 m Lower Murray - Renmark, latitude -34.17435, longitude 140.74688, elevation 22.3 m Mid Murray - Barmah Lake, latitude -36.01912, longitude 144.95732, elevation 103 m Moonie - Alton National Park, latitude -27.99576, longitude 149.33149, elevation 235.3
Productivity	A-SA	Static	National Environmental Stream Attributes v1.1.5	The stream environmental attributes combined with the AGHF Catchment dataset holds values for the "Proportion of stream and valley / sub-catchment / catchment with land-uses where fertiliser is likely to be used". This is a good indicator on the proportion of productivity within the catchment.
Salinity	A-SA	Time Series	Australian Bureau of Meteorology http://www.bom.gov.au/water/hrs/index.shtml	Where recorded gauge data was available from the Bureau of Meteorology online data warehouse, a python script was created to extract daily data using the Kiwis Pie python library. (https://github.com/amacd31/kiwis_pie). The value of electrical conductivity at 25°C was used as an estimate for salinity.
Sediment type	A-SA	Static	Surface Geology of Australia. https://data.gov.au/dataset/surface-geology-of-australia-1-1-million-scale-dataset-2012-edition	River reaches were assigned the value of geological type based on the greatest intersecting length of the reach as compared to the polygon of the geology dataset. All waterbodies were assigned a state of "Good" on the basis that there were holding water and it is expected to contain fine sediments in low flowing areas.

KEV	BBN	Dynamic / static	Source data	Data manipulations
Slope	A-SA	Static	Derived reaches, .GEODATA 9 second DEM and D8: Digital Elevation Model Version 3 and Flow Direction Grid 2008 https://ecat.ga.gov.au/geonetwork/srv/eng/catalog.search#/metadata/66006 Water bodies within 5 km of reaches: SRA Valleys GDA94 (2011)	The slope of reaches were calculated using the average slope from the DEM along the length of the reach. Waterbodies were assigned a slope based on the SRA zone.
Temperature	A-SA	Time Series	Refer to SECTION 1 for details on water temperature modelling.	
Temperature spawning	L-YOY	Time Series		
Temperature zooplankton	L-YOY	Time Series		
Larvae/YOY Temperature	L-YOY	Time Series		

Table S2

Habitat definition for determining location suitability created so as to align the habitat classes defined in Koehn et al. (2016)

Habitat	Definition	Classification
H1	ML/day < maximum base flow < 50% of the average flow values over the entire time-series	Rivers
H2	ML/day >= maximum base flow AND ML/day < maximum cover benches 50-70% of the average flow values over the entire time-series	Rivers
H3	ML/day >= maximum cover benches AND ML/day <= bank full > 70% of the average flow values over the entire time-series	Rivers
H6	Intermittent River red gum floodplain swamp Intermittent Lignum floodplain swamp Intermittent Black box floodplain swamp Intermittent Black box swamp Intermittent Lignum swamps Intermittent River red gum swamps	River Wetland
H7	Permanent wetland Permanent floodplain sedge/grass/forb marshes Permanent high energy upland streams Permanent lowland streams Permanent sedge/grass/forb marshes Permanent transitional zone streams	Wetland

Habitat	Definition	Classification
H8	Temporary wetland Temporary lake Temporary lowland streams Temporary sedge/grass/forb floodplain marsh Temporary sedge/grass/forb marsh Temporary woodland swamp	Wetland
H9	Permanent high energy upland stream Permanent low energy upland stream Permanent lowland stream Permanent stream Permanent transitional zone stream ** these all represent permanently connected wetlands	Wetland
H10	Clay pans Floodplain clay pans Floodplain freshwater meadow Freshwater meadow Temporary floodplain lakes Temporary floodplain wetland Temporary tall emergent floodplain marsh Temporary woodland floodplain swamp	Floodplain
H11	Chowilla Floodplain	Floodplain
H12	Permanent lakes Freshwater Lake Permanent floodplain lakes Permanent floodplain wetland Floodplain Wetland Reservoir Lake Cargelligo	Lake

Habitat	Definition	Classification
H13	Permanent floodplain tall emergent marshes (Cumbung Swamp) Terminal Lakes	Lake

Table S3.

Larvae/Young-of-Year BBN node definitions and states

KEV	Parent / child node	State	Unit	Values	State definition	Notes
Connectivity	Parent	Connected		adult movements upstream and/or downstream can occur	Adult carp have access to move from neighbouring network edges	A Python script was created to review the connectivity of the reach/water body for the post/previous week. If the discharge is over the drown out flow for weirs available, then the spatial unit was deemed connected.
		Unconnected		no adult movements upstream and/downstream can occur	Adult carp have no access to move from neighbouring network edges	
Dissolved Oxygen	Parent	Good	ppm	> 7	Expected higher biomass of carp in waters where dissolved oxygen is above 7 ppm, elicited from experts	
		Moderate		>=2 and <= 7	values elicited from experts	
		Poor		< 2	low biomass of carp in waters where dissolved oxygen is below 2 ppm - elicited from experts	

KEV	Parent / child node	State	Unit	Values	State definition	Notes
Inundation	Parent	High		waterbodies: inundated area > 50% of the waterbody area	waterbodies with areas above 50% would provide a longer-term period for juvenile recruitment to occur	
		Low		waterbodies: inundated area <= 50% of the waterbody area rivers: low where water was present	waterbodies with areas below 50% would provide a shorter-term period for juvenile recruitment	
		No Water		no presence of water		
Location / Location Zooplankton	Parent	High		H6 River wetland, e.g. Barmah–Millewa H9 Wetland permanently connected, e.g. adjacent weir pool H10 Natural floodplain inundation H11 Artificial floodplain inundation, e.g. Chowilla	High presence of zooplankton; heavy vegetation cover and low flows.	The suitability state was allocated after taking a k-Means cluster analysis using Python ScikitLearn KMeans function, based on a number of 3 clusters on the columns of egg, larval,fingerling and young of year survival. The columns representing egg survival, larval survival, fingerling survival and young-of-the-year survival were used for clustering. Table A7.2. Percentage survival elicited from expert opinion and the associated growth rate for

KEV	Parent / child node	State	Unit	Values	State definition	Notes
		Moderate		H7 Wetland perennial, e.g. Kow swamp H8 Wetland ephemeral, e.g. Hattah Lakes H12 Lakes (off-stream), e.g. Lake Victoria H13 Lakes (terminal), e.g. Alexandrina	Moderate presence of zooplankton	each habitat type (Koehn, 2016) 1 Habitat classes assigned to reaches were based upon the flow rates for the week as compared to their individual 50-70 percentile flows for the recorded 17-year period. Whilst habitat classes for water-bodies were static and applied to their types.
		Poor		H1 Main Channel (Mid Upper Murray)—base flow H2 Main Channel (Mid Upper Murray)—cover benches H3 Main Chanel (Mid Upper Murray)—summer irrigation flow H4 Main Channel (Lower Murray)—base flow H5 Main Channel (Lower Murray)—cover benches, summer entitlement H14 Irrigation channels	Low presence of zooplankton; excessively shallow or deep water, no cover and high flows.	

KEV	Parent / child node	State	Unit	Values	State definition	Notes
		No Water		no presence of water		
Photo Period	Parent	Good	hours	>= 10 hours sunlight		"a photoperiod of >10 h and water temperatures >16°C were required for oocyte maturation and ovulation." (Smith, 2004) 2
		Poor		< 10 hours sunlight		
Temperature - Larvae/YOY	Parent	Optimum	°C	>= 20 and <= 28		
		Moderate		>= 16 and < 20 or > 28 and <= 32		
		Poor		< 16 or > 32		
Temperature - Spawning	Parent	Optimum	°C	>= 19 and <= 23		"common carp spawning may occur whenever water temperatures are >16°C for prolonged periods and there is appropriate spawning habitat" (Smith and Walker, 2004)
		Moderate		>= 16 and < 19 or > 23 and <= 28		
		Poor		< 16 or > 28		

KEV	Parent / child node	State	Unit	Values	State definition	Notes
Temperature - Zooplankton	Parent	Optimum	°C	>= 20 and <= 25		
		Moderate		>= 16 and < 20 or > 25 and <= 28		
		Poor		< 16 or > 28		

Table S4.

Adult/subadult BBN node definitions and states

KEV	Parent / child node	State	Unit	Values	State definition
Dissolved Oxygen	Parent	Good	ppm	>= 2	expected higher biomass of carp in waters where dissolved oxygen is above 2 ppm, elicited from experts
		Poor		< 2	low biomass of carp in waters where dissolved oxygen is below 2 ppm - elicited from experts
Downstream Flow	Parent	High	ML/day	Reaches: > 1000 Waterbody classification with inundation: • Temporary • Intermittent • Lake • Floodplain • Meadow • Clay pans	
		Moderate		>= 10 and <= 1000 Waterbody classification with inundation: • Permanent	

KEV	Parent / child node	State	Unit	Values	State definition
		Low		Reaches: > 0 and < 10 Waterbodies: • Reservoir	
		No Flow		Reaches: 0 Waterbodies: • no presence of water	
Productivity	Parent	Good	% of reach catchment	> 95.31	
		Moderate		>= 25.75 AND <= 95.31	
		Poor		< 25.75	
Salinity	Parent	Good	EC@25C (µS/cm) Mean	<= 1800	
		Moderate		> 1800 and < 13,000	
		Poor		>= 13,000	

KEV	Parent / child node	State	Unit	Values	State definition
Sediment	Parent	Good		Reaches: • fine grained • peat swamp • wetland • dam or weir pool • delta • chain of ponds • cut and fill • channel and flood plain alluvium • flood-out • channelised fill • anabranching • lake and swamp deposits; mud, silt • glacial deposits • lacustrine: lagoonal, swamp • poorly consolidated to friable silty sand • sand, fine to medium-grained Waterbodies: all waterbodies were assigned "Good"	Fine alluvial sediments allow for excellent carp feeding

KEV	Parent / child node	State	Unit	Values	State definition
		Moderate		Reaches: • gravel • unconsolidated to poorly consolidated mudstone • siltstone • granite • sandstone • colluvium and/or residual deposits • gravel plains	Sand and coarse materials
		Poor		Reaches: • cobble • gorge • head-water • sinking • urban stream • bluish-grey biotite tonalite • cinder cones - scoria • calcarenite • subaerial caldera volcanic	Cobbles, boulders inhibit carp feeding success
Slope	Parent	Flat	%	Reach < 5 Waterbodies: • Lowland • Upland	For waterbodies states were allocated based on the waterbody area being flat to moderate for the ability to hold water.

<table>
<tr><th>KEV</th><th>Parent / child node</th><th>State</th><th>Unit</th><th>Values</th><th>State definition</th></tr>
<tr><td rowspan="2"></td><td rowspan="2"></td><td>Moderate</td><td rowspan="2"></td><td>>= 5 and <= 25
Waterbodies:
• Montane
• Slopes</td><td></td></tr>
<tr><td>Steep</td><td>> 25</td><td></td></tr>
<tr><td rowspan="3">Temperature - Adults</td><td rowspan="3">Parent</td><td>Optimum</td><td rowspan="3">°C</td><td>>= 16 and <= 28</td><td></td></tr>
<tr><td>Moderate</td><td>>= 7 and < 16
or
> 28 and <= 32</td><td></td></tr>
<tr><td>Poor</td><td>< 7 or > 32</td><td></td></tr>
</table>

Table S5

Lookup table to estimate the biomass density (kg/ha) and numbers of fish for each habitat state x downstream flow combination.

Habitat State	Downstream Flow	Est Adult kg / ha	Est Adult No	Est YOY kg / ha	Est YOY No
High	High	200	128	80	3,636
High	Moderate	150	96	50	2,273
High	Low	100	64	40	1,818
Moderate	High	100	64	40	1,818
Moderate	Moderate	60	38	20	909
Moderate	Low	20	13	10	455
Low	High	20	13	10	455
Low	Moderate	10	6	5	227
Low	Low	5	3	2	91

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SECTION 3 – Demographic Modelling

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Abstract

Common carp (*Cyprinus carpio*) are a serious invasive species of the rivers and other riverine habitats of Australia and several control measures have been proposed, including the release of Cyprinid herpesvirus 3 (CyHV-3). The strategy and potential success of any control measure will be influenced by carp population dynamics and how these dynamics change under varying environmental conditions. Carp survival and their distribution within a catchment depend on abiotic environmental factors, such as water flow rates and availability of habitat type, which vary greatly in space and time. To better understand the underlying drivers of population persistence and define realistic control strategies, we developed a metapopulation model with parameters explicitly linked to spatio-temporal estimates of habitat suitability for carp. This mechanistic (process-based) model provides a basis to evaluate the likely effectiveness of management actions on carp. To demonstrate the use of this model, we evaluated the effects of different reductions to populations for five representative catchments using realised environmental conditions from the early 1990s to 2016 and recording the time taken for the carp population to recover to baseline abundance. We found that recovery time at the metapopulation (catchment) scale can be highly dependent on the flood drought-cycle, with, for example, recovery to 90% baseline values after a severe knockdown event varying from 2 to 10 years between wet and dry periods. In more stable catchments, however, a recovery time (to 90% baseline after a severe event) of ~6 years (range 4-8 years) is more likely. Our results are consistent with the paradigm that carp are a highly successful invasive species, with strong recovery potential, especially during periods of access to quality nursery habitat (i.e. during floodplain and wetland inundation).

Keywords

Biocontrol, common carp, Cyprinid herpesvirus 3, habitat suitability, demography, Murray-Darling basin

Introduction

Common carp (aka carp: *Cyprinus carpio*) are one of the world's most invasive species (Lowe et al. 2000; Koehn 2004) and are a serious ecological issue in Australia. Comprising more than 90% of the estimated fish biomass in some areas (Gehrke et al. 1995), they have become the most abundant large freshwater fish in south-east Australia (Koehn 2004). They are considered to be 'ecological engineers' (Matsuzaki et al. 2009) capable of affecting aquatic ecosystems and, when in high densities, detrimentally impacting benthic habitats, water quality (increased turbidity and nutrient availability) and species abundances and distributions (Gehrke and Harris 1994; Miller and Crowl 2006; Matsuzaki et al. 2009; Weber and Brown 2015). Consequently, carp have been implicated in the degradation of many rivers and wetlands (Koehn et al. 2000). In response, considerable resources have been invested into developing and evaluating control strategies to either eradicate or reduce carp below ecologically impactful levels in Australia (Koehn 2004; Diggle et al. 2011; Brown and Gilligan 2014; Thwaites et al. 2016; Koehn et al. 2017). The most contemporary of these, for example, is the proposed introduction of Cyprinid herpesvirus-3 (CyHV-3) as a biocontrol agent (McColl et al. 2014, 2016). However, environmental conditions in riverine systems in Australia are, by global standards, highly variable across time and space (Bunn et al. 2006; Swirepik et al. 2016) which may affect the growth, spread and population dynamics of carp heterogeneously. Understanding how the population dynamics of carp change in response to variable environmental conditions and concurrent management actions is, therefore, crucial to successful management strategies.

Habitat type, suitability and availability can notably affect carp demographic rates (especially the early life-history-stages) and population dynamics (Weber and Brown 2013; Brown and Gilligan 2014; Bajer et al. 2015; Koehn et al. 2016). While carp are well known for their generalist behaviour and tolerance to a wide range of environmental conditions (Opuszynski et al. 1989; Gehrke and Harris 2001; Stecyk and Farrell 2006; Bajer and Sorensen 2010), spawning and recruitment (to sexual maturity) success in Australian populations is greater during flooding periods when they have access to preferred spawning habitats (e.g. floodplains and shallow lakes; Stuart and Jones 2006a; Conallin et al. 2012), than when flows are low and spawning is confined to the main river channels (Stuart and Jones 2002; Brown and Gilligan 2014; Koehn et al. 2017). These preferred spawning habitats are typically large or rapidly expanding areas with favourable environmental conditions (e.g. moderate temperature, low flow, preferred substrate; Koehn et al. 2016) and low predator densities which promote egg, larvae, and young-of-year survival. Furthermore, increased access to resources in these favourable habitat areas may ease intra-specific competition and reduce the strength of density-dependent mortality (Weber and Brown 2013; Weber et al. 2016). These temporal variations in habitat access for early life-history stages have shown to translate to observable variations in population dynamics, with recruitment pulses and rapid population growth following high-flow/flooding events (Brown et al. 2005; Koehn et al. 2016, 2017). This is especially true for carp populations in Australia, which has, by global standards, highly variable flows across seasons and years (Bunn et al. 2006; Swirepik et al. 2016).

Habitat type and availability is also highly variable across carp's geographic range in Australia, which may lead to spatial variations in population dynamics. Thought to originate from dams in south-eastern Victoria in the 1970s (Koehn 2004), carp have spread to the majority of Australia's largest freshwater catchment, the Murray-Darling Basin (MDB). The MDB covers over 1 million km^2 (~14% of mainland Australia) and extends across five states/territories (see Swirepik et al. 2016 for catchment breakdowns). At a coarse spatial scale, the primary waterway habitats in the MDB vary from patchily connected waterholes in the north (e.g. the Moonie catchment) to wide continuously flowing rivers in the south-east (e.g. the mid-Murray catchment; Swirepik et al. 2016). Within catchments, habitat types are diverse and can include main river channels, wetlands (perennial and ephemeral), shallow and deep lakes, dams and waterholes, tributaries, creeks, and irrigation channels (Koehn et al. 2016; Swirepik et al. 2016; see also SECTION 2). This adds spatial complexity to carp distributions and population dynamics. For example, Ricker stock-recruitment curves fitted to survey data differed among regions of the Lachlan River Catchment, with the major Lakes and upper catchment supporting more recruits (Brown and Gilligan 2014).

Demographic modelling provides the easiest way to evaluate how populations are likely to respond to management actions. Environmental variability is typically included in these models through non-explicit methods (i.e. environmental stochasticity); at each time step in the model, a value for a given parameter (e.g. survival or fecundity) is randomly drawn from a defined distribution (see Brown & Walker 2004, Brown & Gilligan 2014 for carp examples). While this approach recognises that there is variability in the system and provides insight into population dynamics under long-term averaged scenarios, it does not explicitly assign variability to a given time or place. This provides little insight for management regarding how, when and where to best implement which control actions given how the local population is likely to respond under specific environmental conditions. For carp, there has been progress into explicitly including spatio-temporal variation in flow data to better inform management actions. Koehn et al. (2017), for example, varied early life-history traits depending on habitat availability due to flows in three small areas of the Murray River (southern MDB), to show that large-scale removal efforts are more likely to succeed in reducing carp abundance in these areas if they occur during sustained low flow periods. However, it remains unclear whether these results hold true across the range of habitat types present in the MDB.

A key challenge in understanding population dynamics for species such as carp across highly variable landscapes has been a lack of landscape data. Specifically, fine spatial and temporal scale data on habitat type and area and the relative suitability of different habitats for carp at different life-history stages. Habitat suitability modelling has proven a valuable method of developing feasible invasive species management plans (Jiménez-Valverde et al. 2011). Graham et al. (see SECTION 2) combined hydrological modelling, satellite imagery, expert elicitation, and Bayesian Belief Network analysis to develop the first timeseries information of carp habitat suitability across five study catchments of the MBD. Importantly, they cross validated their model with carp biomass estimates. These data, combined data from Koehn et al. (2016) who have estimated the effects of various habitat types on the early life-history stages of fish (within their first year), provide a novel opportunity to evaluate the effects of spatio-temporal environmental variation on carp population dynamic in Australia, and elucidate how this may affect management decisions at the large and fine scale.

Here, we develop a spatially explicit metapopulation model that aims to incorporate the spatio-temporal variation in habitat and flow in the rivers and wetlands of south-eastern Australia. In doing so, we employed two techniques novel to metapopulation modelling. The first explicitly includes habitat suitability estimates in carp demographic parameters to capture the effects of a dynamic environment on carp. The second provides an alternative method to delineating metapopulations structure using community detection analysis from network theory, which is informed by hydrological connectivity data. We demonstrate the use of this model by investigating the response dynamics and persistence likelihood of common carp to a range of knockdown events (moderate: 50% population decline) and a (large: 80% population decline), considering both the degree of knockdown and the timing with respect to hydrological events (e.g. flood vs drought periods). We do this for study five catchments that cover a wide range of riverine habitats in eastern Australia.

Methods

Study Area

To capture the spatial variation across riverine systems in which carp occur in Australia we considered five representative catchment areas in the Murray-Darling Basin (MDB): the Moonie River catchment which borders Queensland and New South Wales, the Lachlan River catchment in central New South Wales, a mid and a lower section of the Murray River, and the Glenelg River catchment in south-western Victoria. These regions were chosen due to the availability of data and expert opinion on local hydrology, and carp ecology, distribution and abundance (see SECTION 1 for more information on the catchments) and span a representative range of carp habitat scenarios (Figure 3.1).

For each of the five catchments we collected weekly time-series data on habitat type and area, and connectivity for all water entities (waterbodies and river reaches, as defined and delineated in SECTION 1). Following Koehn et al. (2016), we categorised water entities into one of eleven habitat types (Table 3.1), based on their flow (reaches) and/or water group type (waterbodies) in a given week. Note that due to data limitations, not all catchments have equal length time-series data, however, all data from all catchments include the Millennial Drought period (grey shading, Figure 3.1) as well as a wetter period.

Delineating Metapopulations (Network Analysis)

We considered fish within each of our five study catchment areas as a metapopulation (a population of connected sub-populations). Based on the classic definition, we define a sub-population as a group of individuals that occupy the same habitat mosaic (defined as a collection of habitat patches; Stanford et al. 2005) and therefore interact with each other (Hanski and Gilpin 1997). Here we use 'mosaic' as the spatial dimension associated with the sub-population rather than the classic 'patch'. This is because a patch is typically a homogenous area, which would relate to individual reaches and waterbodies in our case and this unit is too small for the scale of demographic processes we are considering. Consequently, individuals of the same sub-population experience the same demographic rates (i.e. breeding, density independent survival, and habitat dependent survival), but also influence one another's demographic rates (i.e. density dependent survival). Movement of individuals occurs between sub-populations. We assume that only sub-adults and adults move at the scale of sub-populations, which is reasonable given that otolith chemistry and drift-net catches suggests that carp tend to stay within their natal habitats during their early development stages (Gilligan & Schiller, 2003; Crook & Gillanders, 2006; Stuart &Jones 2006a; Macdonald & Crook 2014). Given that carp demographic rates are linked to habitat type, availability, and suitability, which vary dramatically at a fine spatial scale within catchments (SECTION 2), we required mosaic delineations that were realistic; i.e. mosaics needed to encapsulate entities (reaches and waterbodies) that a fish was likely to have access to, and move between, within a given weekly time-step based on hydrological connectivity and fish movement. To achieve this, we used community detection analysis, a common technique used in network theory to group like nodes (e.g. individuals in social networks) based on their connections (weighted or non-weighted) to other nodes (Fortunato 2010; Javed et al. 2018) (See Figure S2 for a schematic of the process).

We considered individual reaches and waterbodies as nodes in a network (one network for each catchment area), with network edges reflecting the connections between nodes. We used hydrology data and satellite imagery data collect as per SECTION 1 and 2 to determine whether nodes were connected (an edge exists) or not (an edge does not exist) during a given week. We deemed that an edge exists if there was a biologically relevant connection between waterbodies, e.g. if there was water without a significant barrier. Nodes that were never connected during the time series were not included in the network analysis.

For our community detection analysis, we used a random walk algorithm, which works on the premise that an individual randomly walking around a network is more likely to stay within their defined community than leave (Pons and Latapy 2006). Since community detection analysis are time independent, we collapsed time in the network connectivity data. However, to account for the fact that not all connections exist for equal time periods (i.e. some occur the entire time series, while others only exists for a few weeks; Figures S3-S12), we weighted edges by the frequency of connections (the number of times the edge existed: f_e). This reflected the assumption that fish were more likely (at any given point in time) to move between entities that are more frequently connected, making those entities part of the local habitat mosaic. Edges were also weighted by the probability that a fish would travel along the edge (i.e. the relative probability that it would travel at least the distance between the centroids of the entities; K_e), to account for varying sizes in entities. This was determined using a movement dispersal kernel based on published carp movement data (Supplementary Material S1, Stuart & Jones 2006b), with distance being the river distance between centroids of neighbouring reaches, or half the river distance of a reach plus the distance from the centroid of a waterbody to the reach. The algorithm, therefore, favours edges with a higher chance of movement (e.g. small neighbouring reaches) and a higher frequency of connections in the random walk.

To determine the number of steps for the random walk, we used the longest shortest-path in the network (a measure of network diameter). This step size allows a fish the possibility of fully exploring the network in a single ideal walk. It was also important to have a data driven step value as the total number and average length/size of reaches and waterbodies varies among catchments. For example, a fish randomly walking 3 steps (entities) in a catchment with an average entity length of 100km would travel a greater distance than one in a catchment where the average entity length is 10km. The random walk community detection algorithm is not appropriate for directed networks (Pons and Latapy 2006). Consequently, we assumed the network to be undirected and that fish could move either direction along an edge. Where there was a notable one-way barrier to fish movement (i.e. a waterfall) we assumed no movement rather than two-way movement.

We ran the network analysis in R, using the *igraph* package (version 1.0.0), which includes the random walk community detection algorithm. Reaches and waterbodies were then assigned to mosaics based on their community groupings. Connectivity between mosaics over time (i.e. connected or not in a given week) were based on the connectivity between the nodes linking mosaics.

Modelling Demography

We defined five life-history-stages for carp, reflecting major transitions in survival, fecundity, and mobility rates: larvae, two young-of-year stages, sub-adults and adults (Figure 3.2). Young-of-year was broken into two stages to capture the transitional period from larvae to true young-of-years, all of which have different demographic rates (Koehn et al. 2016, 2017). Adults are defined as sexually mature fish. Each week in the model, fish survive and either grow to the next stage-class or remain in their current stage-class, and older stages (sub-adults and adults) move between sub-populations. The average time spent in each stage class is based on published knowledge about carp growth and maturation (Vilizzi and Walker 1999; Ronsmans et al. 2014; Koehn et al. 2016, 2017). Density-dependent juvenile survival is common in both fresh-water and marine fish, and evidence suggests that it exists in Australian (Koehn et al. 2000; Brown and Gilligan 2014) and North American (Weber and Brown 2013; Bajer et al. 2015; Caskenette et al. 2018) carp populations. We, therefore, assumed that fish experience density dependent survival until they are adults. All parameter and variable descriptions can be found in Table 3.2.

Metapopulation dynamics were described using a matrix model, based on the vec-permutation matrix approach developed by Hunter and Caswell (2005). In its simplest form the model can be written as

$$\mathbf{n}_{t+1} = \mathbf{M}\mathbf{n}_t$$

where $\mathbf{M}$ is the metapopulation projection matrix and $\mathbf{n}_t$ is a vector of the fish abundance in the metapopulation at time *t*. Following Hunter and Caswell (2005), $\mathbf{M}$ is a function of both demographic and dispersal processes such that

$$\mathbf{M} = \mathbf{P}^{\mathbf{T}}\mathbb{D}_t\mathbf{P}\mathbb{B}_t$$

where $\mathbb{B}_t$ and $\mathbb{D}_t$ are block diagonal matrices respectively containing the demographic and movement rates at time *t*, and $\mathbf{P}$ is the vec-permutation matrix. The block diagonals on the matrices $\mathbb{B}_t$ and $\mathbb{D}_t$ are 5 x 5 (5 stages) and z x z (z sub-populations) projection matrices for the demography of population *i* ($\mathbf{B}_{h,i,t}$) and movement of stage *a* ($\mathbf{D}_{a,t}$).

Survival & growth

Survival and growth of carp in sub-population *i* at time *t*, is described as

$$\mathbf{B}_{h,i,t} = \begin{bmatrix} (1-G_1)P_{1,i,t} & 0 & 0 & 0 & F_{i,t}P_{1,i,t} \\ G_1P_{1,i,t} & (1-G_2)P_{2,i,t} & 0 & 0 & 0 \\ 0 & G_2P_{2,i,t} & (1-G_3)P_{3,i,t} & 0 & 0 \\ 0 & 0 & G_3P_{4,i,t} & (1-G_4)P_{4,i,t} & 0 \\ 0 & 0 & 0 & G_4P_5 & P_5 \end{bmatrix},$$

where G_a is the probability that a fish in age class *a* will grow and move to the next stage class, and $P_{a,i,t}$ and $F_{i,t}$ is the per-capita weekly survival of fish in stage class *a* and the production and survival of eggs to hatching, in sub-population i, at time t, respectively. The probability of transitioning between stages (G_a) is inversely proportional to the average time (in weeks) spent in each stage (Table 3.2).

We capture environmental variation in our model through 1) habitat associated density-independent survival rates of eggs to sub-adults (following Koehn et al. 2016, 2017) and 2) variable effects of density dependence on the survival rates of larvae to sub-adults, driven by habitat suitability. Here we assume that once fish reach sexual maturity their survival is robust to changes in their environment. This dual approach to including environmental variability recognises that environmental variations are likely to impact an individual fish's survival both independently of (e.g. variable salinities affecting juvenile survival rates; Whiterod and Walker 2006) and due to its conspecifics (e.g. competition for limited resources; Koehn et al. 2000; Brown and Gilligan 2014). For the habitat associated density independent survival rates, we used survival rates for eggs to sub-adult carp previously estimated for the defined habitat types (Table 3.2; Koehn et al. 2016), weighted by the proportion of habitat type associated with each sub-population at a given time-step.

A key concept in ecology is population regulation, which prevents it from growing unchecked. In single-species modelling, regulation is commonly captured through density-dependent mechanisms that reflect the tendency for populations to self-regulate via processes such as cannibalism and resource competition (White et al. 2010). Density-dependence is often mechanistically modelled as a function of population abundance (or biomass) normalised by the area available to the population, where area reflects the amount of resources available. However, habitat quality is also important in regulating populations as regions of highly suitable habitat will provide more resources per capita per area unit than regions of low suitability (Hodgson et al. 2009). To account for habitat quality affecting population regulation, we included the modelled habitat suitability data from SECTION 2 into the density dependent survival functions of larvae to sub-adults. To translate the habitat suitability data from qualitative and categorical (i.e. "low"/"high"; see SECTION 2) to quantitative and continuous (which is mathematically tractable), we used expert elicitation to assign young-of-year and sub-adult/adult abundances to the habitat suitability categories (as was done in the validation section of SECTION 2). Per-capita weekly survival of larvae (a = 1), young-of-year (a = 2 & a = 3), and sub-adults (a = 4) can, therefore, be described as

$$P_{a,i,t} = \sum_{h=1}^{13} H_{h,i,t}\, S_{a,h}\; e^{-c_1 \frac{\sum_{b=a}^{5} N_{b,i,t}}{Y_{i,t}}}, a \in [1,3]$$

$$P_{4,i,t} = S_4\; e^{-c_2 \frac{\sum_{b=4}^{5} N_{b,i,t}}{A_{i,t}}}.$$

Here, $S_{a,h}$ is the per-capita density independent survival rate of fish stage a in habitat type h and $H_{h,i,t}$ is the proportion of habitat type h (as classified in Table 3.2) associated with sub-population i at time t; $Y_{i,t}$ and $A_{i,t}$ are the estimated abundances of larvae/YOY and sub-adult/adult carp in sub-population i, at time t, based on habitat suitability estimates alone; and c_1 and c_2 are density dependence parameter values that indicated the strength of density effects on the survival of first year fish (larvae and young-of-years; 1) and sub-adults (2). As there are currently no empirical estimates for the density dependence parameters (c_1 and c_2), we set values that yielded stable spatio-temporally averaged abundance estimates across all catchments similar to those predicted by habitat suitability alone. This is a valid assumption, given that the habitat suitability modelling well reflected the relational trends seen in predicted biomass estimates (see model validation in SECTION 2). We also considered a doubling and halving of the paired density dependent parameter values, which covered the range of model scenarios in which the metapopulation performs better (equilibrates above) and worse (declines below) than the estimates that are based on habitat alone. Adult per-capita survival is independent of habitat type or density dependence and, as such, $P_5 = S_5$.

Carp spawning is protracted, occurring largely during the non-winter months with major peaks in spring and late summer (Sivakumaran et al. 2003; Smith and Walker 2004a, b). To capture these dynamics and distribute spawning over time, we developed a spawning distribution function, which integrates to 1 over 52 weeks. A bimodal Gaussian distribution, with 60% of the recruits occurring within the first peak and 40% in the second, well described peaks in spawning aggregations predicted from the habitat suitability modelling (SECTION 2, Figures S13-S14). The production and survival of eggs ($F_{i,t}$) is, therefore, a product of the fecundity of adult fish (f), the spawning distribution kernel (Φ_t), and the habitat averaged survival of eggs in sub-population i at time t, such that

$$F_{i,t} = f\ \Phi_t \sum_{h=1}^{11} H_{h,i,t}\ S_{0,h}$$

$$\Phi_t = \frac{0.6}{\sigma\sqrt{2\Pi}}\ e^{\frac{-(t-t_{max1})^2}{2\sigma^2}} + \frac{0.4}{\sigma\sqrt{2\Pi}}\ e^{\frac{-(t-t_{max2})^2}{2\sigma^2}},$$

Where $H_{h,i,t}$ is the proportion of habitat type h, associated with sub-population i at time t, and $S_{0,h}$ is the proportion of eggs that survive in habitat type h (Table 3.2).

Movement

We assume that only sub-adult and adult fish move between sub-populations, and that movement is driven by a combination of sub-adult/adult density, resource availability, and random movements. The movement matrices ($\mathbf{D}_{a,t}$) for larvae and the young-of-year stages are, therefore, zero matrices. For sub-adults and adults, $\mathbf{D}_{a,t}$ is a non-zero matrix who's elements equal the proportion of fish that leave sub-population i and move to j at time t ($m_{j,i,t}$).

We break movement into three conceptual parts, where $m_{j,i,t} = K_{i,t}\ L_{i,t}\ p_{j,i,t}$.

- *The likelihood that a fish will move out of the sub-population, based on the size of the sub-population*. Using a movement kernel based on published carp movement data (Supplementary Materials S1, Stuart and Jones 2006b) we first determined the probability that a fish will move the length of the habitat mosaic associated with the sub-population or further (which equal one minus the cumulative density function, see below). Given that mosaics are made up of a complex set of reaches and waterbodies we used the river distance defined above in the Delineating Metapopulations section, summed over all reaches and waterbodies in the sub-population, as a measure of mosaic length. The probability of moving out of sub-population i at time t given the size of sub-population i at time t (dispersal kernel; $K_{i,t}$) is, therefore,

  $$K_{i,t} = 1 - \left(\frac{1}{2} + \frac{1}{2}\ \mathrm{erf}\left[\frac{\ln(l_i) - 1.16}{\sqrt{2*2.17}}\right]\right),$$

  where l_i is the length of the mosaic associated with sub-population i.

- *The effect of local density and habitat suitability on the probability that a fish will leave the sub-population*. Next, we assumed that fish experience a trade-off between the quality and the quantity of resources available: they are attracted towards areas of high habitat suitability, but away from areas of high density. Conceptually, this means that an area with highly suitable sub-adult/adult habitat may attract more fish, but as densities increase, fish are more likely to leave. To capture this, we developed a measure of per-capita resource availability for carp in sub-population i at time t. $R_{i,t}$, which is defined as

  $$R_{i,t} = \frac{A_{i,t}}{\sum_{b=4}^{5} N_{b,i,t}},$$

  where $\sum_{b=4}^{5} N_{b,i,t}$ is the total number of sub-adults and adults. As before, $A_{i,t}$ (the abundance of sub-adult/adult carp in sub-population i, at time t, estimated from habitat suitability modelling) is a proxy for resource availability. If $R_{i,t} = 1$ then there is equal resources to carp in that sub-population and week. If the number of carp in a sub-population is greater than the resource availability (i.e. $\sum_{b=4}^{5} N_{b,i,t} > A_{i,t}$) then $R_{i,t} < 1$ and, on average, carp will have less than the desired amount of resources (i.e. the sub-population is overcrowded). If $R_{i,t} > 1$, then there is a surplus of resources. Whether an individual decides to leave a sub-population depends on $R_{i,t}$ relative to neighbouring sub-populations, such that the proportion of fish that will leave sub-population i, at time t ($L_{i,t}$) is defined as

  $$L_{i,t} = 1 - \frac{R_{i,t}}{\max(\Gamma_{R,i,t})},$$

  where $\Gamma_{R,i,t}$ is the set of all $R_{i,t}$ values in the defined neighbourhood (sub-population i and all connected first-order neighbours). If sub-population i has the highest $R_{i,t}$ value that week, then fish will not leave the sub-population (since $R_{i,t} = \max(\Gamma_{R,i,t})$).

- The distribution of fish leaving a given sub-population among all connected neighbouring sub-populations, based on habitat suitability. Last, of the fish that leave sub-population i, a proportion will go to each of the directly neighbouring sub-populations which are connected at time t. To determine this distribution, we assumed that sub-populations with a higher habitat suitability will attract a greater proportion of migrants. The proportion of fish leaving sub-population i that go to j, at time t ($p_{j,i,t}$), is therefore

  $$p_{j,i,t} = \frac{A_{j,t}}{\mathrm{sum}(\Gamma_{A,i,t})},$$

  where $\Gamma_{A,i,t}$ is the set of all $A_{i,t}$ values in the defined neighbourhood (sub-population i and all connected first-order neighbours).

We assume fish movement is non-directional; an individual can move upstream as easily as downstream. This is a reasonable assumption given that there is currently no strong evidence correlating the direction of adult movements to flows (discharge rates or water levels) or temperature (Stuart & Jones 2006a, Osborne et al. 2009, Jones & Stuart 2009). Furthermore, telemetry and mark-recapture studies suggest nearly equal movements in carp in both directions from release sites for carp in Australia (Reynolds 1983, Stuart & Jones 2006a, Jones & Stuart 2009), as well as for Koi in New Zealand (Osborne et al. 2009). However, this may not always be true, especially when there are significant barriers to upstream movements, such as weirs. Here we took a conservative approach and assumed that a barrier to one-way movement was a barrier to all movement. From a demographic perspective, this is unlikely to significantly affect the dynamics of established metapopulations.

Model Runs

The demographic model was run with baseline values (Table 3.2) for each of the five study catchments to establish time-series of baseline abundance values. The dates over which the models were run (i.e. model run times) varied depending on the Habitat Suitability Modelling time-series data (Table S2). Model runs, however, always started at the beginning of July in the first year to avoid initialising the model during the breeding season.

Demographic model outcomes, especially discrete-time models, can be sensitive to the initial population structure (i.e. the relative proportion of fish in each stage class and sub-population). To avoid these model artefacts, we ran the model for a 15-year burn-in period to establish initial metapopulation structure. During this burn-in period we used values for $H_{h,i,t}$, $Y_{i,t}$, and $A_{i,t}$, averaged over the 3 months prior to the model start date. We then combined the resulting stage structures with abundance estimates from the Habitat Suitability Modelling (taken at the demographic model's start date) to determine our initial model conditions. We did this for all catchments except the Glenelg, for which habitat suitability data precede the likely date of arrival of carp into the lower river system (below Rocklands Weir). Carp are thought to have occurred in Rocklands Reservoir since the early 1990s, but not to have entered the rest of the catchment until 2001 (Thwaites et al. 2016). To capture this dynamic we ran the Glenelg model with a small number of adults in Rockland Reservoir at the beginning of the time-series (100 adults in 1991) and introduced carp into each sub-population at the start of 2001 (10 carp per sub-population).

To simulate a knockdown event, we implemented a pulse mortality event that removed 80% of the metapopulation in a single week, spread evenly across the metapopulation. To evaluate the effects of environmental conditions on the recovery dynamics we ran 50 replicate simulations with knockdowns occurring on different randomly chosen (without replacement) dates during the time series. We then compared abundances post knockdown to the baseline values (without any knockdown) to determine recovery rates - i.e. at 50% recovery, abundance is half what it would have been at that point in time if there was no knockdown, not half the abundance at the time of knockdown. We did this since baseline abundances fluctuate independently of knockdown due to environmental conditions. We did this for each of the five study catchments. We also considered a moderate knockdown event, where 50% of the population experiences mortality. We also tested the sensitivity of our outcomes to our strength of density dependent values (c_1 and c_2).

Model Validation

To validate the model, we compared relevant model outputs (abundance and biomass density from our baseline model) to two independent datasets; 1) empirical count data from electrofishing surveys undertaken in the Lachlan (2007 to 2011) and Lower Murray Catchments (2003 to 2017) , both datasets were extracts from the NSW Freshwater Fish Research Database (FFRD), (henceforth referred to as the 'empirical count data'; Dean Gilligan, pers. comms.), and 2) estimated biomass densities from the NCCP Biomass Project (henceforth referred to as the 'Biomass Project density data'; Stuart et al., 2019). We considered the model to be valid if it 1) captures well the temporal dynamics present in the empirical count data and 2) reflects well carp densities estimated by the Biomass Project. This performance criteria tests whether the model is fit for its purpose; to capture realistic carp dynamics and provide a tool test the effectiveness of alterative management strategies.

Comparing abundances over time

For the empirical count data, electrofishing surveys were only conducted in limited sites across the Lachlan (n = 18) and Lower Murray (n = 23) catchments and at non-consistent times during the year (although sampling was primarily done during summer and spring in the Lachlan (Gilligan et al., 2010). Furthermore, not all sites were sampled every sampling period (e.g. every year). To account for this in comparing the empirical count data to our model abundances, we matched the sampled sites to habitat mosaic areas from our delineated metapopulations and sampled our model for the same regions and months (for the Lower Murray) and years (for the Lachlan) as present in the empirical count data. We then normalised model abundances by the associated habitat mosaic area divided by 0.3 ha, the average area sampled in the electrofishing surveys (Gilligan et al. 2010). Given the low sample numbers, we averaged counts over each month for both datasets, and over space where more than sampling site occurred within a given habitat mosaic.

Comparing biomass densities over space

We obtained shapefiles containing biomass density estimates in week 20, 2011 across the five catchments from the Biomass Project (Stuart et al., 2019). Given that the underlying object files delineating reaches and waterbodies used by the Biomass Project differed from that used in our Hydrology modelling (SECTION 1), we only compared biomass densities at intersecting entities. We then aggregated biomass densities estimates from the Biomass Project to the habitat mosaic/sub-population level to match the scale of our demographic modelling. To test the goodness-of-fit between the two datasets we fit a linear regression, with the biomass densities from our model as the y-variable and the Biomass Project density data as the x-variable (following Pineiro et al. 2008). The associated coefficient of determination (R^2) indicates how much variation in one data set is explained by variation in the other, and the slope and intercept of the line fitted describe the consistency and model bias, respectively (Smith and Rose 1995; Mesple et al. 1996). These parameters can be formally tested by evaluating whether the slope and intercept significantly differ from 1 and 0, respectively. We also calculated the root mean squared deviation (RMSD; Pineiro et al. 2008);

$$RMSD = \sqrt{\frac{1}{n-1} \sum_{i=1}^{n} \left(d_i^* - d_i\right)^2}$$

where d_i^* and d_i are the biomass density estimates from the demography model and the Biomass project, respectively, and n is the total number of data points (n = 121 across the 5 catchments). RMSD estimates the mean deviation between the datasets (Pineiro et al. 2008), in the same units as the considered variable (biomass density; $kg.ha^{-1}$).

Results

Network Analysis

The network analysis was able to delineate the catchments into demographically and epidemiological relevant metapopulations (Figures 3.3-3.4). The total number of sub-populations varied between catchments, with the highest in the Lachlan (50), followed by Lower Murray (29), Mid Murray (27), the Moonie (15), and the Glenelg (10).

Variations in catchment structure and connectivity were detected across the five catchments. The Mid and Lower Murray, and the lower (western) parts of the Lachlan, were characterized by many waterbodies that connect to the main river channel during flooding or other high-water events (producing the 'starburst' effects in graphs a, Figures 3.3-3.4). In these catchments, sub-populations are defined by habitat mosaics that contain many entities (>50) which are typically made up of a section of the main river channel that maintains a base level of habitat area, and many wetland, lake, and floodplain areas that dramatically change in area over time (see Figures S15-S19 for habitat area by sub-population). Mosaics in the upper (east) Lachlan, however, have few entities; mainly rivers and large lakes. Sub-populations in the Moonie are is characterized by mosaics containing a moderate number (10-40) of rivers, streams, and wetlands, all of which are highly variable in area. The Glenelg had many waterbodies that were not detected as connecting to the main river channel (had no water) at any point in time (Glenelg graph A, Figure 3.3-3.4). Consequently, mosaics in this catchment are made up of a handful (<10) of river reaches, with two including major lakes. Connectivity between sub-populations in the Lower and Mid Murray, and the Glenelg was typically high, with connections occurring >75% of the time. The Moonie, in contrast, had infrequent (<25% of time) connections. Connectivity among sub-populations in the Lachlan was patchy, with a few sub-populations connected for nearly the entire time-series, and others not connected at all (graphs b, Figures 3.3-3.4).

Baseline Model

Modelled baseline carp dynamics, for both larvae/young-of-year (L/YOY) and sub-adult/adult (SA/A) abundances, varied markedly across the five study catchments, with large-scale (decadal) boom-bust dynamics in the Lachlan and Glenelg catchments, fine-scale (1-2 year) fluctuations in the Moonie catchment, and more stable dynamics (with pulse events) in the Mid and Lower Murray catchments (Figure 3.5). Importantly, the Glenelg metapopulation reflects population growth dynamics typical of an invading species; initial exponential growth, which slows once resources (as indicated by the abundances estimated from the habitat suitability modelling; orange lines in Figure 3.5) become limited and density dependence regulates the population (panels G, Figure 3.5).

The Millennial Drought (~2001 - 2010) affected the Lachlan and Glenelg metapopulations suppressing recruitment (panels L and G, left-hand-side, Figure 3.5) and notably reducing SA/A abundances (panels L and G, right-hand-side, Figure 3.5). The drought, however, had minor impacts on the Mid and Lower Murray metapopulations; primarily preventing large recruitment years due to floodplain inundation events (panels MM and LM, Figure 3.5), and had no notable effect on the Moonie catchment (panels M, Figure 3.5). The Moonie catchment, however, was subject to yearly flood-drought cycles, which produced fine-scale temporal variations in abundances between years (panels M, Figure 3.5).

At the sub-population level, modelled population dynamics (here indicated by sub-adult and adult abundances) varied markedly within catchments (Figures 3.6-3.10). This was especially true for the Lachlan, Mid Murray and Lower Murray catchments (Figures 3.6, 3.8, & 3.9). Sub-populations dynamics were typically well characterised by their major habitat types. For example, sub-populations with more stable populations (e.g. sub-populations 1, 23, 42, and 43 in the Lachlan metapopulation, Figure 3.6) were typically main river channels with consistent baseline flows (see Figures S15-S19 for habitat area by sub-population). Conversely, more dynamic sub-populations coincided with shallow lakes that varied dramatically in area (e.g. sub-populations 50 and 16 in the Lachlan metapopulation, Figure 3.6) or floodplains (e.g. sub-population 17 and 24 in the Lower Murray metapopulation, Figure 3.8) (see Figures S15-S19 for habitat area by sub-population). Movement of fish also had a minor influence on the modelled dynamics of sub-populations. This was especially true in the Lachlan catchment directly after the Millennial Drought period, when pulse recruits moved from the floodplains (e.g. sub-population 3, Figure 3.6) into adjoining rivers (e.g. sub-population 6, 28 and 35, Figure 3.6), temporally increasing the local densities.

Knockdown Scenarios

After an acute knockdown, recovery to 90% of the baseline was quick, averaging 5.2-6.5 years for all catchments for a severe (80% reduction) event, and 2.3-5.7 years for a moderate (50% reduction) event (horizontal bars, right column, Figure 3.11). Metapopulation recovery was fastest within the first few years. Under a severe knockdown scenario (80% KD), for example, majority of scenarios across all catchments recovered from 20% (at time of knockdown) to 70% baseline within 3 years (top row, middle column, Figure 3.11).

While mean time to recovery percentage was not dissimilar between catchments (max 2.5 years difference), there was notable variation in the range of recovery times between catchments (grey shaded violins and coloured points, Figure 3.11). This reflects the sensitivity of the catchment to the timing of the knockdown. The Moonie, and Mid and Lower Murray catchments were relatively less sensitive to the date of knockdown, with narrower ranges (<4 years) of recover times for both moderate and severe knockdown scenarios. The Lachlan and Glenelg catchment, however, had notably larger ranges of recovery times: 2 - 12 years, for example, for the Glenelg to recovery to 90% baseline values after a severe knockdown (80% KD) depending on when the knockdown occurred (right column, top row, Figure 3.11).

For the Lachlan and Glenelg catchments, recovery times were notably longer when the knockdown occurred immediately before, or during a drought/low flows period (characterised by low habitat area, see Knockdown Date panel Figure 3.11), and shorter when the knockdown preceded or occurred during a wet/high flows period (characterised by high habitat area, see Knockdown Date panel Figure 3.11). For example, time to 90% recovery after a severe knockdown (80% KD) for the Lachlan metapopulation was 9 - 11 years when the knockdown occurred prior to 2005 (dark blue-green markers, right column, top row, Figure 3.11) and recovery was during the Millennial Drought period, but 2 - 4 years when the knockdown was after the drought broke in 2010 (lime green markers, right column, top row, Figure 3.11). Importantly, the recovery dynamics after knockdown were not sensitive to our c_1 and c_2 values (Figures S20-S21).

Model Validation

Both the demographic model and the empirical count data are highly variable in both space and time and consistent trends are not strong (Figure 3.12). However, peaks in abundances are noticeable in the empirical count data at the end of the millennial drought (~2011), in the young-of-year and sub-adults in the Lower Murray (lower right panel, Figure 3.12), and in the sub-adults in the Lachlan (upper right panel, Figure 3.12) and this is reflected in the demographic model (left panels, Figure 3.12). Similarly, a lesser peak in young-of-year abundances 2006 in the Lower Murray in the empirical data is also reflected in the demography model, however the model also has sub-adult abundances peaking at this time, yet this is not reflected in the empirical data (lower panels, Figure 3.12). For both catchments, abundance values from the demographic model (which have been adjusted to be comparable to the area sampled by the electrofishing surveys) are consistently greater for the young-of-year and adults, and lower for the sub-adults, compared to the empirical catch data (Figure 3.12).

At a given point in time (week 20, 2011), the demographic model reflects well carp densities estimated by the Biomass Project (Figure 3.13). The slope (1.11) and intercept (36.5) of the fitted linear regression do not significantly differ from 1 ($p = 0.242$) and 0 ($p = 0.104$), respectively, and the adjusted R^2 value is 0.556. The mean deviation between the datasets is 141.20 kg.ha^{-1} (RMSD). At the catchment level, there is greater variation in biomass density values in our demographic model compared to the Biomass Project's data for all catchments except the Lachlan and Glenelg (Figure 3.13).

Discussion

Here we develop a carp metapopulation model that builds upon the current scientific understanding of the species and explicitly includes realised fine-scale habitat data that spans over 20 years. We also used network analysis in a novel way to delineate an ecologically meaningful metapopulation structure that is data-driven. Importantly, this model provides a strong foundation on which to evaluate the relative efficacy of various management options for carp. We demonstrate this by evaluating the recovery dynamics of carp metapopulations in five study catchments in response to a severe and a moderate knockdown event. We found that large scale temporal variations in habitat (e.g. flood-drought cycles) had a notable impact on recovery times, with drought periods increasing recovery times for carp up to five-fold (~2 to 10 years) in highly dynamic areas (i.e. the Lachlan and Glenelg catchments), while having minimal impact (max 4 years variation) in the relatively more stable catchments (for 90% recovery from a severe knockdown; Figure 3.11). Fine scale temporal environmental variations (i.e. seasonal variations), however, had little effect on recovery times, which averaged ~6 years across catchments.

Our results are consistent with the paradigm that carp are a highly successful invasive species, with strong recovery potential, especially during periods of access to quality nursery habitat (i.e. during floodplain and wetland inundation). We explicitly demonstrate this in our study by 1) evaluating the recovery times after knockdown scenarios, and 2) through the modelled population growth in the Glenelg River catchment. Importantly, our modelled dynamics reflect realistic population growth rates, as demonstrated by the results for the Glenelg River catchment. Carp entered the Glenelg River (below Rockland Reservoir) around 2001 but were thought to have comparatively slower population growth than in other regions of the MDB due to limited recruitment sites (Thwaites et al. 2016). A 2014-15 catch survey estimated an average density of 43 kg/ha (range = 4-121 kg/ha, varying by site/reach; Thwaites et al. 2016). These dynamics reflect those in our model, in which all sub-populations below Rocklands Reservoir (sub-populations 1-8 & 10) grew towards capacity (as set by the habitat suitability estimates, orange lines; Figure 3.10), with an average density in the same order of magnitude as the empirical estimates (34 kg/ha, range = 21-52 kg/ha varying by sub-population). That the demographic model and empirical catch estimates are both below those predicted by the habitat suitability modelling (63 kg/ha; range = 43-121 kg/ha varying by sub-population) agrees with the intuition that the Glenelg catchment has limited preferred nursery sites and carp populations will hence do less well. This was also reflected by the lack of connected wetlands and floodplains in the habitat modelling (Figure S19). Importantly, the same model parameter values were applied to Glenelg as other catchments, the only variations being the catchment specific habitat and hydrology time-series data.

Our baseline model also reflects the consensus amongst carp population biologists that floodplain inundation and increased access to habitats of high spawning and recruitment success (typically due to by high flow events) promote ‘booms’ in carp abundances, which are especially noticeable in recruitment pulses (Gehrke et al. 1995; Brown et al. 2005; King et al. 2010; Koehn et al. 2016). In our model, this was especially noticeable at the sub-population scale, where dramatic increases in local habitat areas resulted in increases in larvae and young-of-year. At the metapopulation scale, however, increased spawning habitat area did not always translate to clear peaks in metapopulation abundances. At this scale, the predicted abundances that have built up in the more stable main river channels of the catchment overwhelm the pulse recruitment events that are associated with floodplain/wetland inundation events. The notable exceptions are the Lachlan River and Glenelg River catchments, where a large proportion of the catchment area is characterised by temporally dynamic lakes that support large numbers of carp during wetter periods (Figures 3.1 & 3.5).

Our results highlight the importance of scale when considering carp population dynamics and management scenarios. For carp there has been significant work done in the Lower Murray and Barmah-Millewa Forest regions. Demography and flows data from these sites have informed the model underpinning Koehn et al. (2017), who evaluate the efficacy of different carp management (mainly manual removal) scenarios under a range of flow regimes. Koehn et al. (2017) focused on three small-scale case sites containing a major lake or floodplain, treating each as a closed population (equivalent in size to sub-populations in our model). They found that large-scale removal of adults from lakes, especially during low flow periods, may be a useful control measure. However, given the high connectivity through the main river channel of the Lower Murray (panel LM, Figure 3.1), and the relative stability of the metapopulation as a whole (Figure 3.5), there may be a strong rescue effect between sub-populations. Consequently, the degree and scale to which carp need to be removed for this management action to be effective may be greater than expected. It's important to note that we used the same habitat dependent first year survival rates as Koehn et al. (2017). Conversely, our findings suggest that the expected efficacy of proposed management strategies (e.g. carp removal and biocontrol options) in the Lachlan River catchment may be currently underestimated (Brown and Gilligan 2014). Brown and Gilligan (2014) used a metapopulation structure with large-scale (1300-6200 ha) sub-population delineations (aka 'zones'). Within zones fish were assumed to move, breed and interact homogenously. However, results from our network analysis demonstrate that, at this scale, Brown and Gilligan's (2014) zones typically include sub-populations that are infrequently connected (Panel L graph b, Figure 3.3). Therefore, the effects of sustained drought periods, when connectivity along the main river channel is low, may play a greater role in managing carp in the Lachlan than expected.

A novel outcome from our study is the use of community detection analysis, adapted from social network theory, to delineate river systems into an ecologically meaningful metapopulation. This approach allowed us to apply an objective, data-driven methodology that was consistent across all catchments and resolved issues with previous river metapopulation models that delineated sub-population regions based on physical structures or genetics (Brown and Gilligan 2014). Community detection analysis has been used previously to define metapopulation patches in large kelp habitats (Cavanaugh et al. 2014) and delineate metapopulations of generic sessile marine invertebrates (Jacobi et al 2012). This is, however, the first known attempt to combine network theory with geo-spatial, hydrological, and movement data to delineate fish metapopulations. Previously, only the Lachlan catchment had been assigned a metapopulation structure, with zones (aka sub-populations) defined based on the presence of significant barriers to fish passage and natural habitat boundaries (Brown and Gilligan 2014). Our approach builds on this by including movement kernel data (i.e. the probability that a fish will move a given distance) with connectivity (hydrological connections) and barrier data to defined habitat mosaics (defining the spatial bounds of sub-populations) that represent areas in which fish are more likely to stay than leave. For the Lachlan, these areas are smaller and more numerous than the zone definition (8 zones compared to 50 sub-populations). Importantly, movement between sub-populations in our model was also driven by the movement kernel and physical connectivity, as well as habitat suitability, rather than movement rates based on population persistence (as was used in Brown and Gilligan 2014).

We tested our model against two independent datasets to assess whether our model is fit for its defined purpose; to capture realistic carp dynamics and provide a tool test the effectiveness of alterative management strategies. Our findings suggest that our model is valid, in that it captures aspects of the temporal dynamics present in empirical count data recorded in electrofishing surveys and reflects well carp densities estimated by the Biomass Project. However, additional datasets would help strengthen validation as there several key caveats with the data used. With respect to the empirical count data, a major issue for both the Lachlan and the Lower Murray data is the low sample sizes and inconsistent sampling across space and time, and a short time series that predominantly spans the drought period in the Lachlan. Furthermore, electrofishing is also known to be biased against larger and smaller carp (Brown et al 2005) and this may partly explain why our model abundances are consistently higher than the empirical catch data values for the young-of-year and the adults, but lower for the sub-adults. An alternative explanation may relate disparities between how we have categorised stage-classes; in our model transitions between stages is based on age, while empirical data classifies transitions on sizes (<150mm = young-of-year; 150-400mm = sub-adults; >400mm = adults). With respect to the Biomass Project density data, it is important to note that these biomass density estimates are modelled estimates, extrapolated from local samples and catch data to the nation-wide scale. Consequently, they are subject to several key assumptions and represent an alternative estimate to our data, rather than a true empirical estimate for validation. However, the degree of agreement between the two models for the date considered is encouraging. The major caveat here is that only one point is time (week 20, 2011) is considered. We recommend more validation exercises be undertaken if other validation datasets become available.

It is important to recognise that all models are potentially sensitive to assumptions made regarding the underlying mechanics of the model (e.g. the structure of the model equations used) and these are highly challenging to test or validate without long-term data under various scenarios (Oreskes et al. 1994;

Jakeman et al. 2006). While care was taken to use data collected with high confidence for model parameter values, errors in the data underlying model parameter estimates are likely to have propagated through the model. A key parameter for future consideration is the density-independent survival rates for <1-year-old fish, which were based on expert elicitation (Koehn et al. 2016) and still require empirical observations to validate. A sensitivity analysis of our model will help determine parameter values that require further scrutiny, and this is planned for future works. Consequently, exact quantitative predictions from our models should be approached with caution.

It is well accepted in the peer-reviewed and grey literature that environmental variation, in particular river hydrology, is likely to play an important role in the management of carp in Australia (Bunn et al. 2006; Brown and Gilligan 2014; Koehn et al. 2016, 2017; Stratford et al. 2016). Consequently, including habitat variation has become an important goal of carp metapopulation models (Brown and Gilligan 2014; Stratford et al. 2016; Koehn et al. 2017). To date, these models have been constrained by 1) a paucity of data, being either temporally limited to simulating random variations in environmental fluctuations (versus realised time-series data on flows, temperature, habitat etc.) or, more commonly, spatially limited to specific small-scale study sites; and 2) the challenge of explicitly translating habitat variations into biologically meaningful terms (i.e. model expressions and parameter values). Furthermore, these issues are often combined. Here we present an alternative model that addresses these issues using large-scale habitat suitability data and a novel approach to delineating metapopulations. We provide a means to explore management options at both the fine and coarse scale and use it to demonstrate the range of spatiotemporal variations in carp population dynamics that can be expected in carp in the MDB. An important next step in this work is to use our model to explicitly evaluate the efficacy of various proposed management strategies, while considering the environmental variability present in Australian carp populations.

Acknowledgements

We gratefully acknowledge the National Carp Control Plan (FRDC 2016-170) for funding the research reported here.

We thank Ivor Stuart and Matt Jones (Arthur Rylah Institute) for the provision of the historical dataset from the tagging study undertaken in the Barmah Forest during 1999-2000; Stuart Little (Murray–Darling Basin Authority) for facilitating access to the Murray River PIT tag dataset; Paul Brown (La Trobe Uni) and Dean Gilligan (DPI NSW) for feedback on the model structure and carp life-history traits and providing data for the validation exercises; and to Stephen Taylor (CSIRO-Data61) for improvements and curation of the *R* code developed to run the demographic model.

Tables

Table 3.1

Habitat type categories used across all study catchments. Based on Koehn et al. (2016).

Code	Habitat Type	Description	Grouping
H1	Main Channel: base flow	Low level not topped up by irrigation flows <50% bankfull. Only occurs during severe drought	River
H2	Main Channel: cover benches	50–70% bankfull irrigation flow	
H3	Main Channel: bankfull	70% to bankfull irrigation flow	
H6	River Wetland	Adjacent low-lying wetlands (without broader floodplain inundation)	River Wetland
H7	Wetland: perennial	Off-stream wetlands with permanent water (e.g. Barren Box Swamp)	Wetland
H8	Wetland: ephemeral	Off-stream wetlands, high elevation wetlands dry out if not reconnected	
H9	Wetland: permanently connected	Weir pools at operating height, low flows	
H10	Floodplain: natural inundation	Broad floodplain inundation (as per high-level natural flood)	Floodplain
H11	Floodplain: artificial inundation	Inundated by regulators	
H12	Lake: off-stream	Permanent waterbodies (e.g. Lake Cargelligo)	Lake
H13	Lake: terminal	Permanent waterbodies at the end of the system	

Table 3.2

Parameter descriptions, values, and references (where applicable) used in the baseline carp demography model.

<table>
<tr><th>Parameter</th><th>Symbol</th><th>Value</th><th>Source</th></tr>
<tr><td>Fecundity of adult fish</td><td>f</td><td>250000</td><td>(Stratford et al. 2016 Table 6; Koehn et al. 2016 Table A8.1)</td></tr>
<tr><td>Width (standard deviation) of spawning peaks (weeks)</td><td>σ</td><td>4</td><td>SECTION 2 (spawning suitability)</td></tr>
<tr><td>Middle of first spawning peak (weeks after July 1st)</td><td>t_{max1}</td><td>18</td><td>SECTION 2 (spawning suitability)</td></tr>
<tr><td>Middle of second spawning peak (weeks after July 1st)</td><td>t_{max2}</td><td>39</td><td>SECTION 2 (spawning suitability)</td></tr>
<tr><td>Probability of growing and leaving stage class a, $a \in [1,4]$</td><td>G_1
G_2
G_3
G_4</td><td>1/3
1/3
1/46
1/406</td><td>(Vilizzi and Walker 1999; Ronsmans et al. 2014; Koehn et al. 2016)</td></tr>
<tr><td>Annual per-capita density independent survival of eggs (0), larvae (1), and young-of-year 1 (2) and 2 (3) fish in habitat h (see Table 1). Note, annual survival rates have been converted into weekly survival rates for larvae and young-of-year</td><td>$S_{a,h}$</td><td>
<table>
<tr><th>h</th><th>$S_{0,h}$</th><th>$S_{1,h}$</th><th>$S_{2,h}$</th><th>$S_{3,h}$</th></tr>
<tr><td>H1</td><td>0.007</td><td>0.263</td><td>0.321</td><td>0.942</td></tr>
<tr><td>H2</td><td>0.014</td><td>0.337</td><td>0.389</td><td>0.945</td></tr>
<tr><td>H3</td><td>0.025</td><td>0.374</td><td>0.410</td><td>0.953</td></tr>
<tr><td>H6</td><td>0.121</td><td>0.464</td><td>0.598</td><td>0.960</td></tr>
<tr><td>H7</td><td>0.047</td><td>0.414</td><td>0.592</td><td>0.959</td></tr>
<tr><td>H8</td><td>0.080</td><td>0.385</td><td>0.552</td><td>0.946</td></tr>
<tr><td>H9</td><td>0.065</td><td>0.403</td><td>0.529</td><td>0.967</td></tr>
<tr><td>H10</td><td>0.109</td><td>0.434</td><td>0.588</td><td>0.967</td></tr>
<tr><td>H11</td><td>0.122</td><td>0.488</td><td>0.513</td><td>0.971</td></tr>
<tr><td>H12</td><td>0.052</td><td>0.390</td><td>0.508</td><td>0.958</td></tr>
<tr><td>H13</td><td>0.064</td><td>0.422</td><td>0.532</td><td>0.962</td></tr>
</table>
</td><td>(Koehn et al. 2016)</td></tr>
<tr><td>Weekly pre-capita density independent survival of sub-adults (4) and adults (5)</td><td>S_4
S_5</td><td>$0.37^{\frac{1}{52}}$
$0.80^{\frac{1}{52}}$</td><td>(Stratford et al. 2016 Table 6; Koehn et al. 2016 Table A8.1)</td></tr>
<tr><td>Strength of coupled low, medium, and high density dependence on first-year fish (larvae and young-of-years; 1) and sub-adults (2).</td><td>c_1
c_2</td><td>[0.04, 0.08, 0.16]
[0.15, 0.30, 0.60]</td><td>NA; see main text</td></tr>
<tr><td>Proportion of habitat type h (relative to the total available habitat) associated with sub-population i at time t</td><td>$H_{h,i,t}$</td><td>variable over time and sub-population, bounded by [0, 1]</td><td>SECTION 2 (averaged over 6-weeks)</td></tr>
</table>

Estimated abundance of larvae/YOY (Y) and sub-adult/adult (*A*) carp from habitat suitability alone, in sub-population *i*, at time *t*	$Y_{i,t}$ $A_{i,t}$	variable over time and sup-population	SECTION 2 (averaged over 6-weeks)

Figures

Figure 3.1

Summary of habitat availability (area) by type (colours; left panel) and connectivity between water entities (right panel) in each of the five study catchments over the available time-series. Letters indicate catchment name; Moonie (M), Lachlan (L), Mid Murray (MM), Lower Murray (LM), and Glenelg (G). Grey shading indicates the Millennial Drought period, which predominately affected south-eastern Australia, including the Murray-Darling Basin. The lighter brown in panel LM indicates Lake Victoria

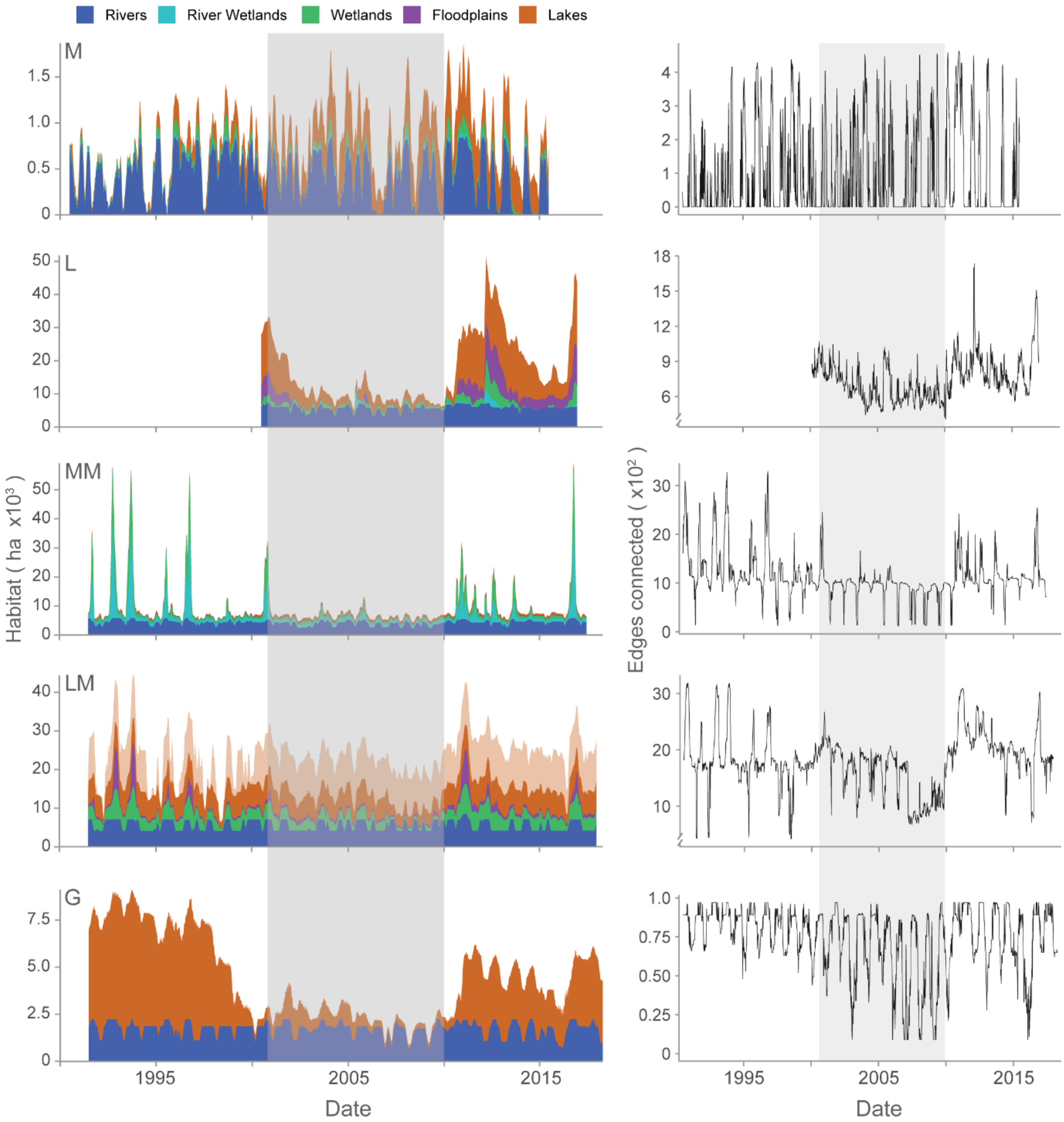

Figure 3.2

Carp life-cycle diagram representing the transition through the life-stages and key demographic processes captured in the models. For each demographic process, the relevant time-varying parameter is noted. For example, density dependent sub-adult survival is a function of adult habitat suitability [DD survival: $f(HS_A)$]. Numbers in parenthesis indicate the average time a fish spends in each stage-class and is, therefore, subject to the stage-relevant demographic processes.

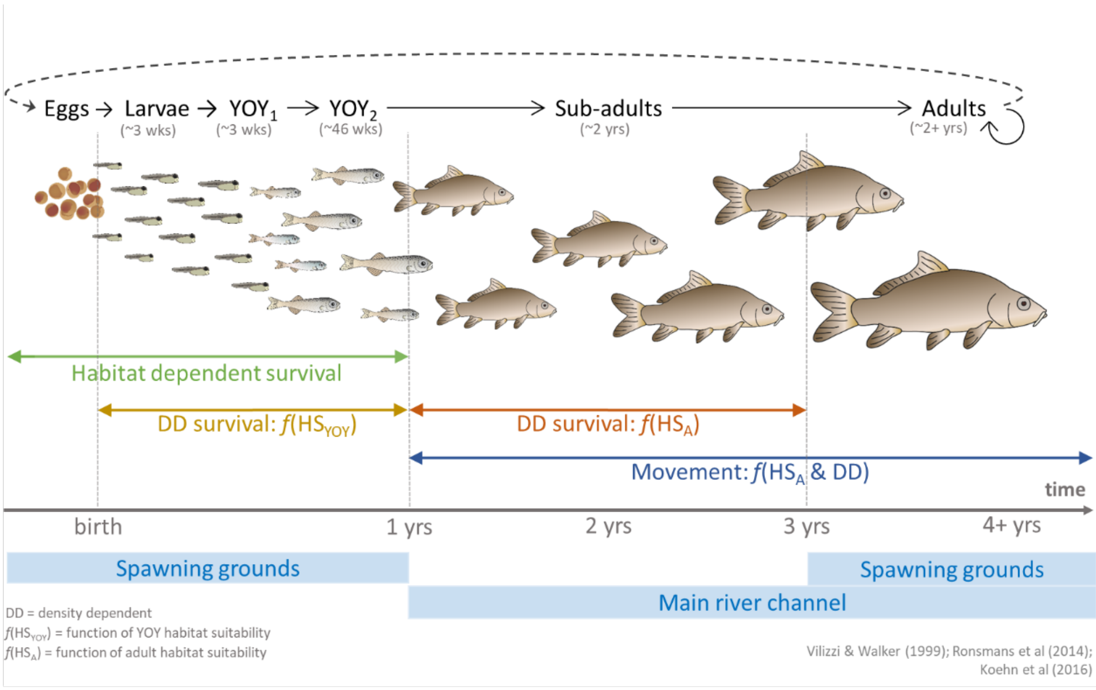

Figure 3.3

Network representations (a) and the resulting metapopulation graphs (**b**) of the Lachlan River (L), Glenelg River (G) and Moonie River (M) catchments. For graphs **a**, nodes (points) represent reaches and waterbodies, and edges (lines) represent connections between reaches and waterbodies. For graphs **b**, nodes represent sub-populations (grouped reaches and waterbodies) and edges, connections between sub-populations. Integers indicate sub-population number (as determined by the community detection analysis). Edge colour indicates the frequency of connection between nodes (the percentage of time that the edge exists in the time-series). Where an edge is not present, there is no connection detected between those two nodes at any time during the study period. Note that scale is relative within catchments, but not between catchments.

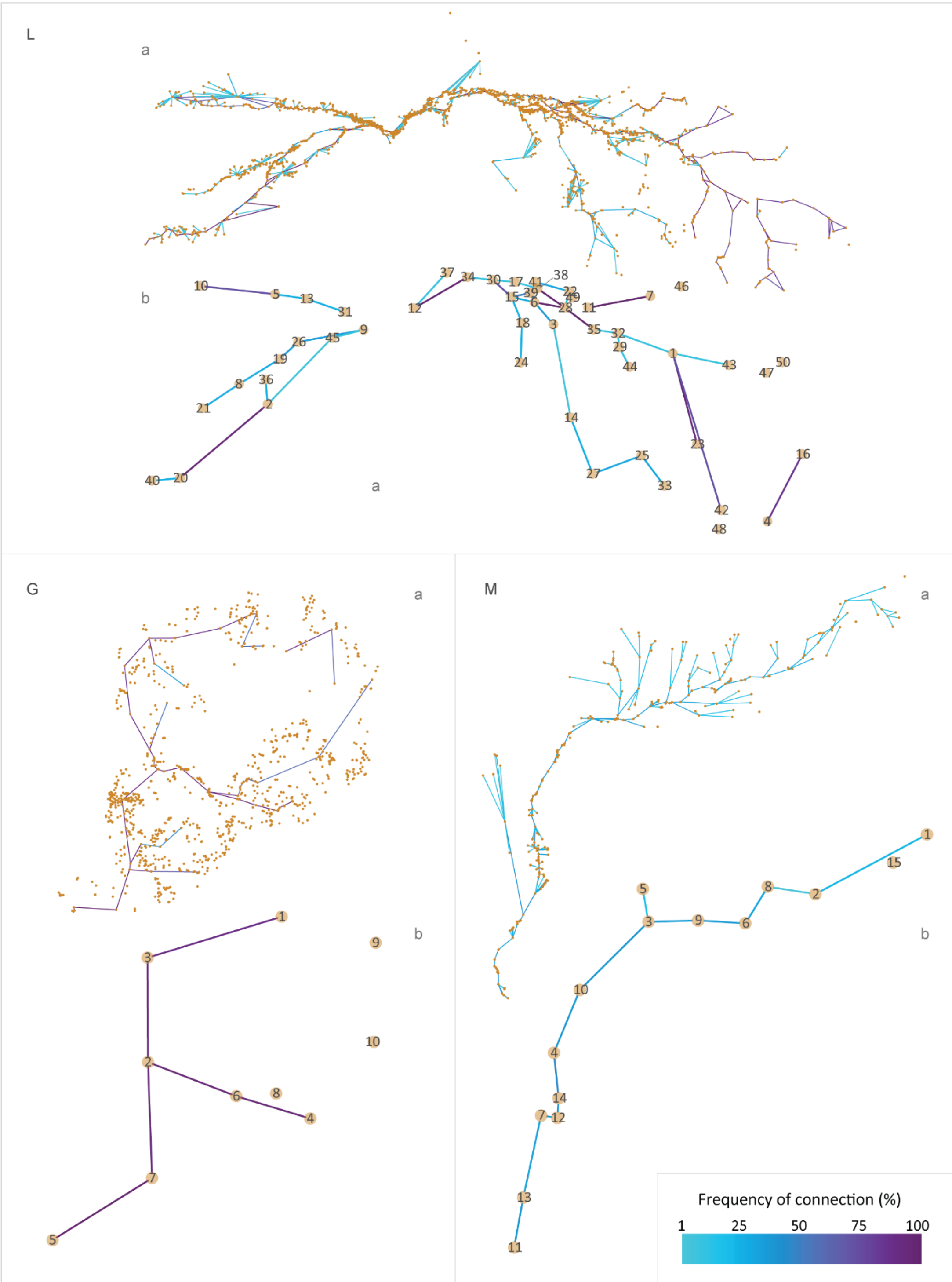

Figure 3.4

Network representations (a) and the resulting metapopulation graphs (b) of the Mid Murray (MM) and Lower Murray (LM) River catchments. For graphs a, nodes (points) represent reaches and waterbodies, and edges (lines) represent connections between reaches and waterbodies. For graphs b, nodes represent sub-populations (grouped reaches and waterbodies) and edges, connections between sub-populations. Integers indicate sub-population number (as determined by the community detection analysis). Edge colour indicates the frequency of connection between nodes (the percentage of time that the edge exists in the time-series). Where an edge is not present, there is no connection detected between those two nodes at any time during the study period. Note that scale is relative within catchments, but not between catchments.

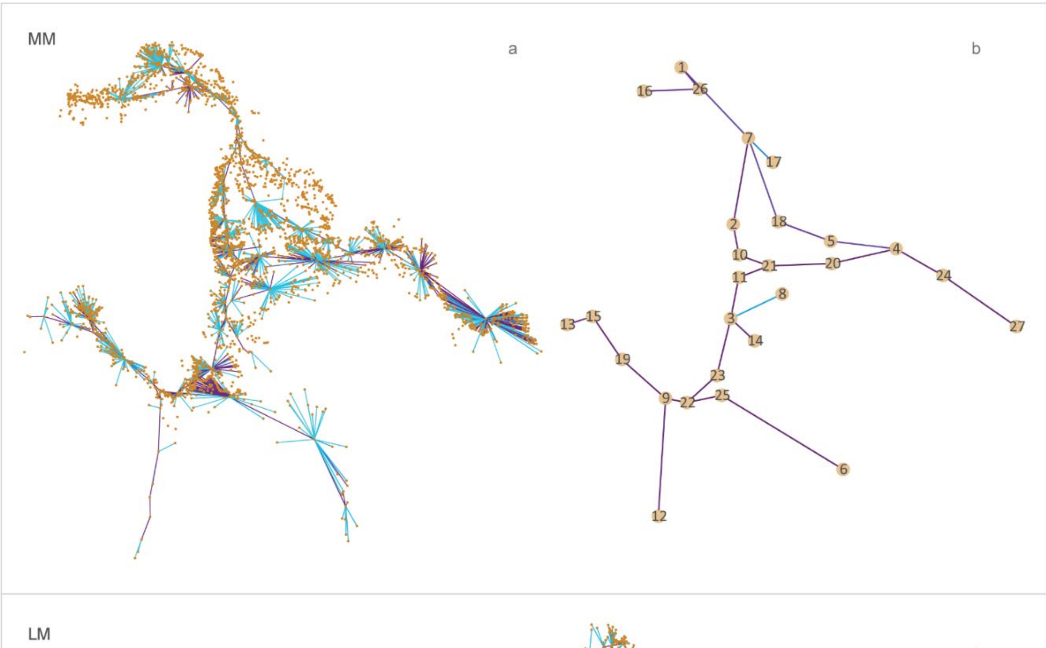

Figure 3.5

Baseline modelled abundances (black lines) of larvae and young-of-year (YOY; left panel) and sub-adult and adult carp (right panel) in each of the five study catchment areas, compared to abundances estimated based on habitat suitability alone (orange lines). Grey shading indicates the range of density dependence values considered in our demography model, from half to double baseline values. Letters indicate catchment name; Moonie (M), Lachlan (L), Mid Murray (MM), Lower Murray (LM), and Glenelg (G).

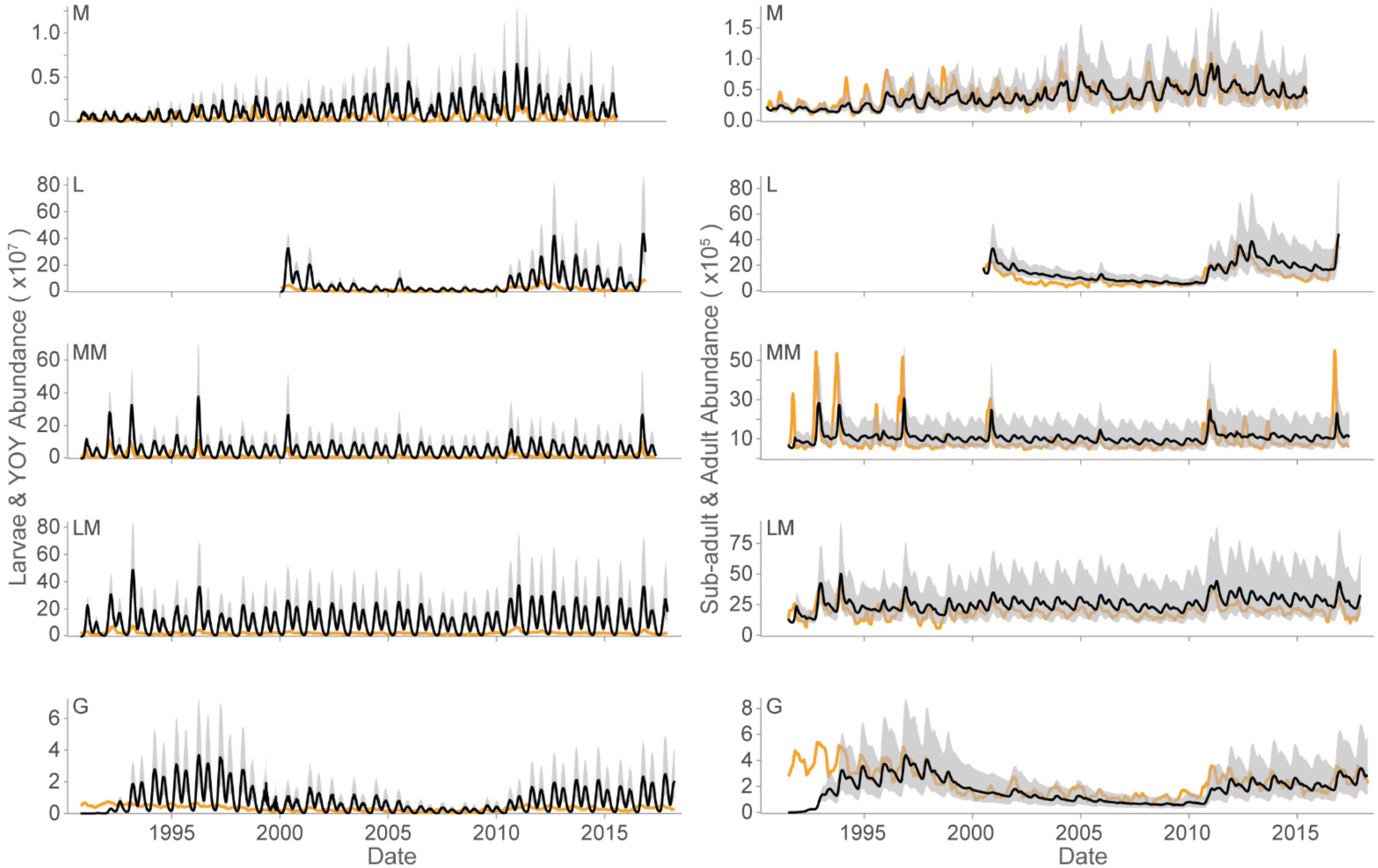

Figure 3.6

Baseline modelled abundances (black lines) of sub-adult and adult carp in the defined sub-populations of the Lachlan River catchment, compared to abundances estimated based on habitat suitability alone (orange lines). Grey shading indicates the range of density dependence values considered in our demography model, from half to double baseline values. Bold number indicate sub-population number, with numbers in parenthesis indicating neighbouring sub-populations. For sub-population number reference see Figure 3.3.

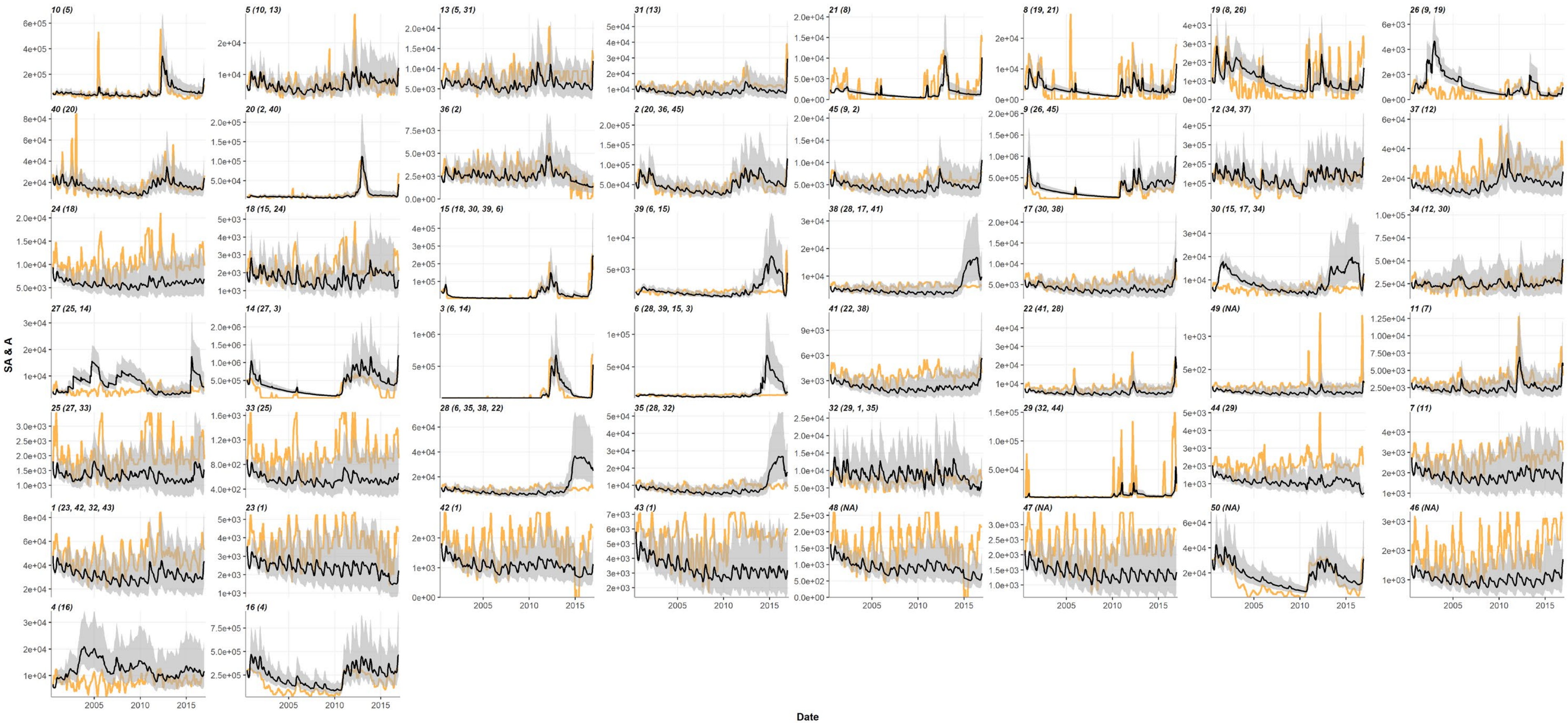

Figure 3.7

Baseline modelled abundances (black lines) of sub-adult and adult carp in the defined sub-populations of the Moonie River catchment, compared to abundances estimated based on habitat suitability alone (orange lines). Grey shading indicates the range of density dependence values considered in our demography model, from half to double baseline values. Bold number indicate sub-population number, with numbers in parenthesis indicating neighbouring sub-populations. For sub-population number reference see Figure 3.3.

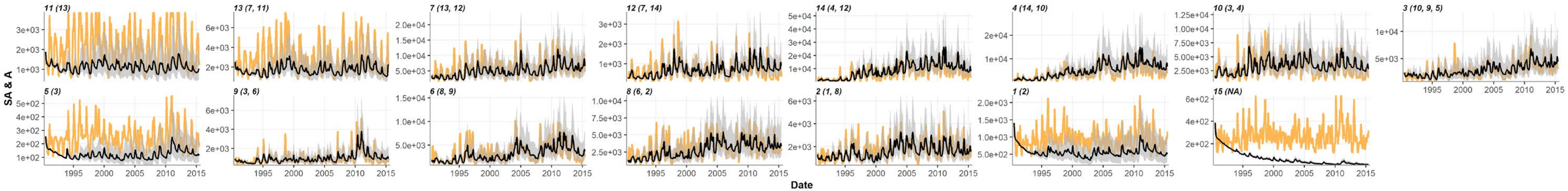

Figure 3.8

Baseline modelled abundances (black lines) of sub-adult and adult carp in the defined sub-populations of the Lower Murray River study area, compared to abundances estimated based on habitat suitability alone (orange lines). Grey shading indicates the range of density dependence values considered in our demography model, from half to double baseline values. Bold number indicate sub-population number, with numbers in parenthesis indicating neighbouring sub-populations. For sub-population number reference see Figure 3.4.

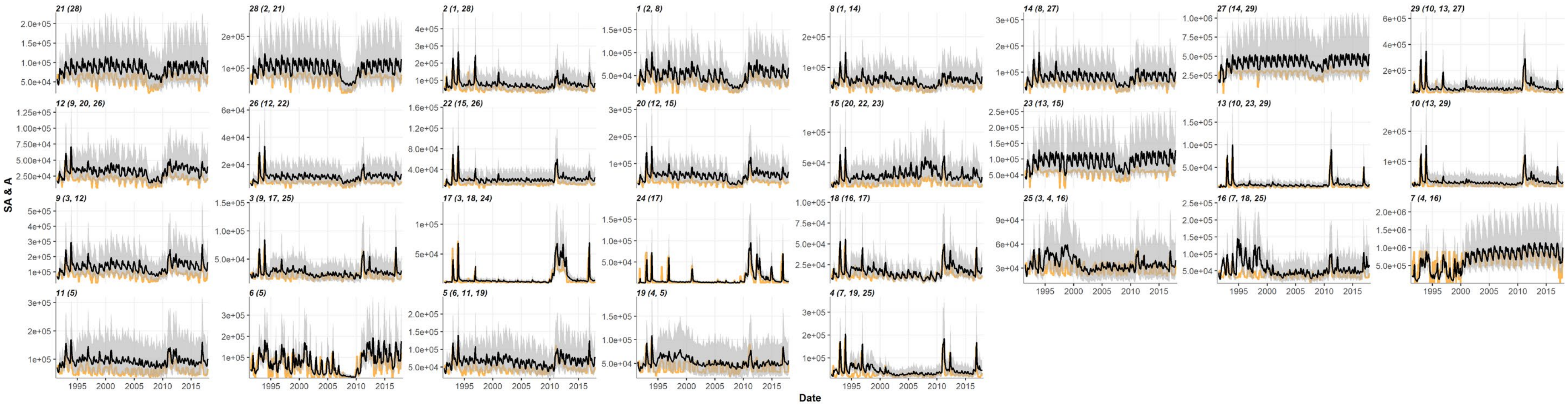

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Figure 3.9

Baseline modelled abundances (black lines) of sub-adult and adult carp in the defined sub-populations of the Mid Murray River study area, compared to abundances estimated based on habitat suitability alone (orange lines). Grey shading indicates the range of density dependence values considered in our demography model, from half to double baseline values. Bold number indicate sub-population number, with numbers in parenthesis indicating neighbouring sub-populations. For sub-population number reference see Figure 3.4.

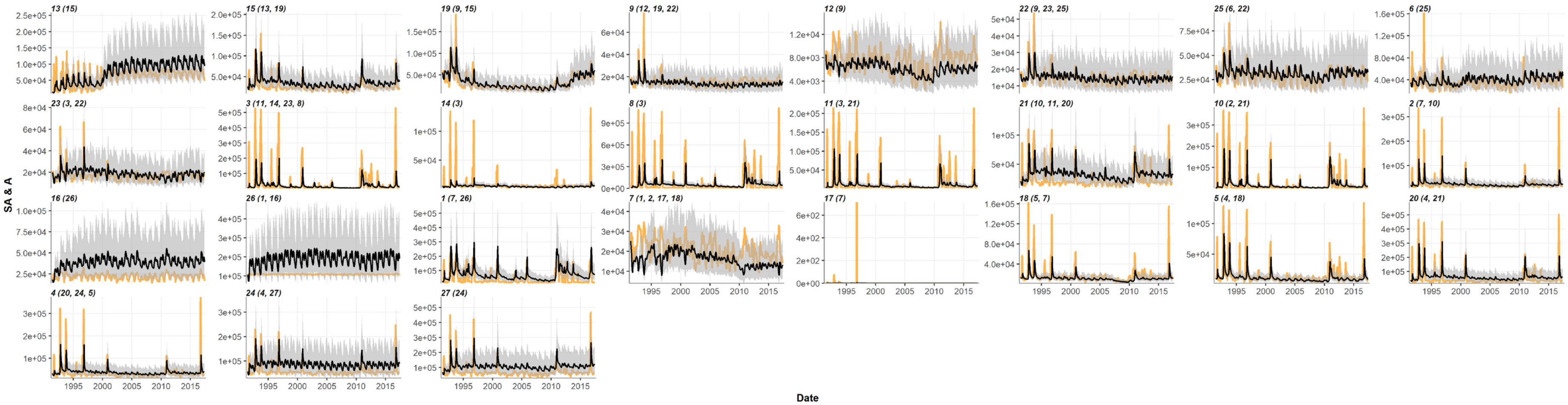


Figure 3.10

Baseline modelled abundances (black lines) of sub-adult and adult carp in the defined sub-populations of the Glenelg River catchment, compared to abundances estimated based on habitat suitability alone (orange lines). Grey shading indicates the range of density dependence values considered in our demography model, from half to double baseline values. Bold number indicate sub-population number, with numbers in parenthesis indicating neighbouring sub-populations. For sub-population number reference see Figure 3.3.

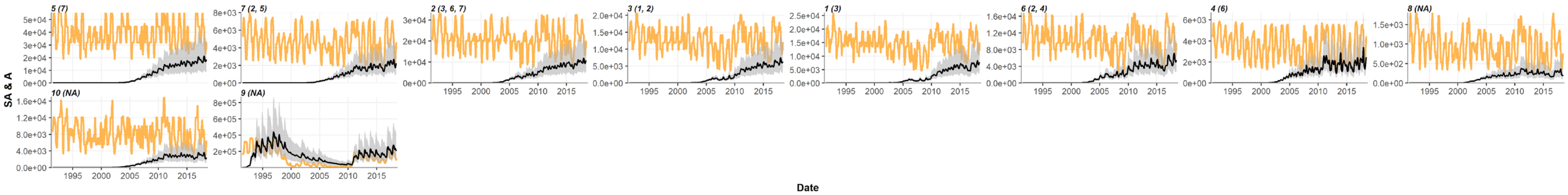


Figure 3.11

Time (in years) to percentage recovery (50%, 70%, or 90%) following an acute knockdown that reduced the metapopulation by 80% (top row; 80%KD) and 50% (second row; 50%KD), for each of the five study catchments. Note, percentage recovery is measured as the proportional difference between the knockdown scenario and the baseline scenario in a given week. Coloured points are individual scenario runs (50 replicates), with colours relating to the date of knockdown (and the corresponding changes in total habitat in hectares over the subsequent recovery period) as per the Knockdown Date insert. Grey shaded violins show the distribution of data for each scenario, with examples in the Distribution of Data insert. Horizontal bars indicate average times for each scenario. Letters indicate catchment name; Moonie (M), Lachlan (L), Mid Murray (MM), Lower Murray (LM), and Glenelg (G).

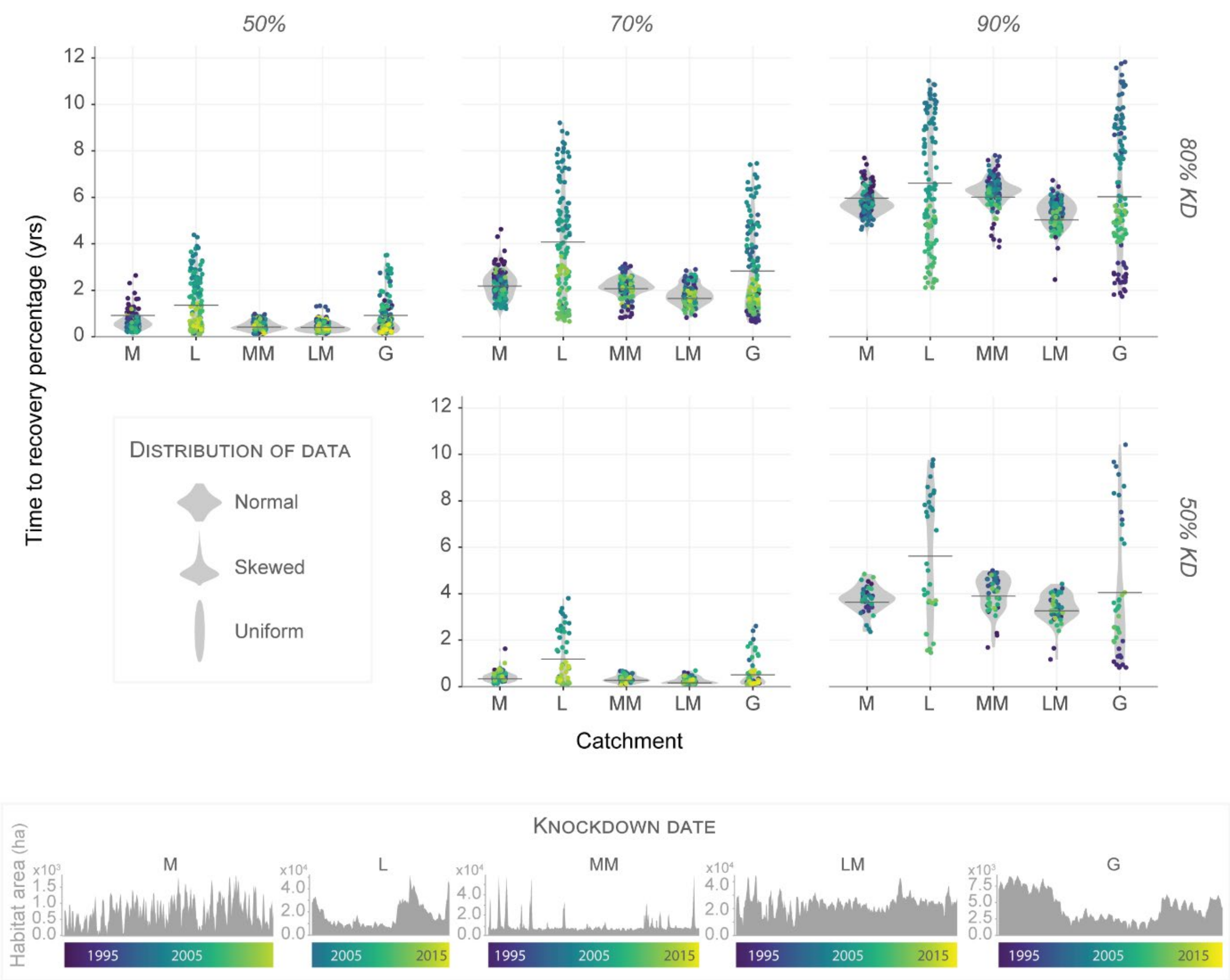


Figure 3.12

Yearly abundances for the Lachlan River (top panels) and Lower Murray River (bottom panel) catchments as output by the demographic model (left panels) and collected in electrofishing surveys (right panels), for young-of-year (YOY), sub-adults (SA), and adults (A). Boxplots show the median, quantile and outlier values aggregated across months and locations (within catchments), and grey bars indicate mean values. For the demographic model, abundance values have been rescaled to match the standard sampling area of electrofishing, and only sub-populations and months that match empirical sampling areas/times are reported (see methods).

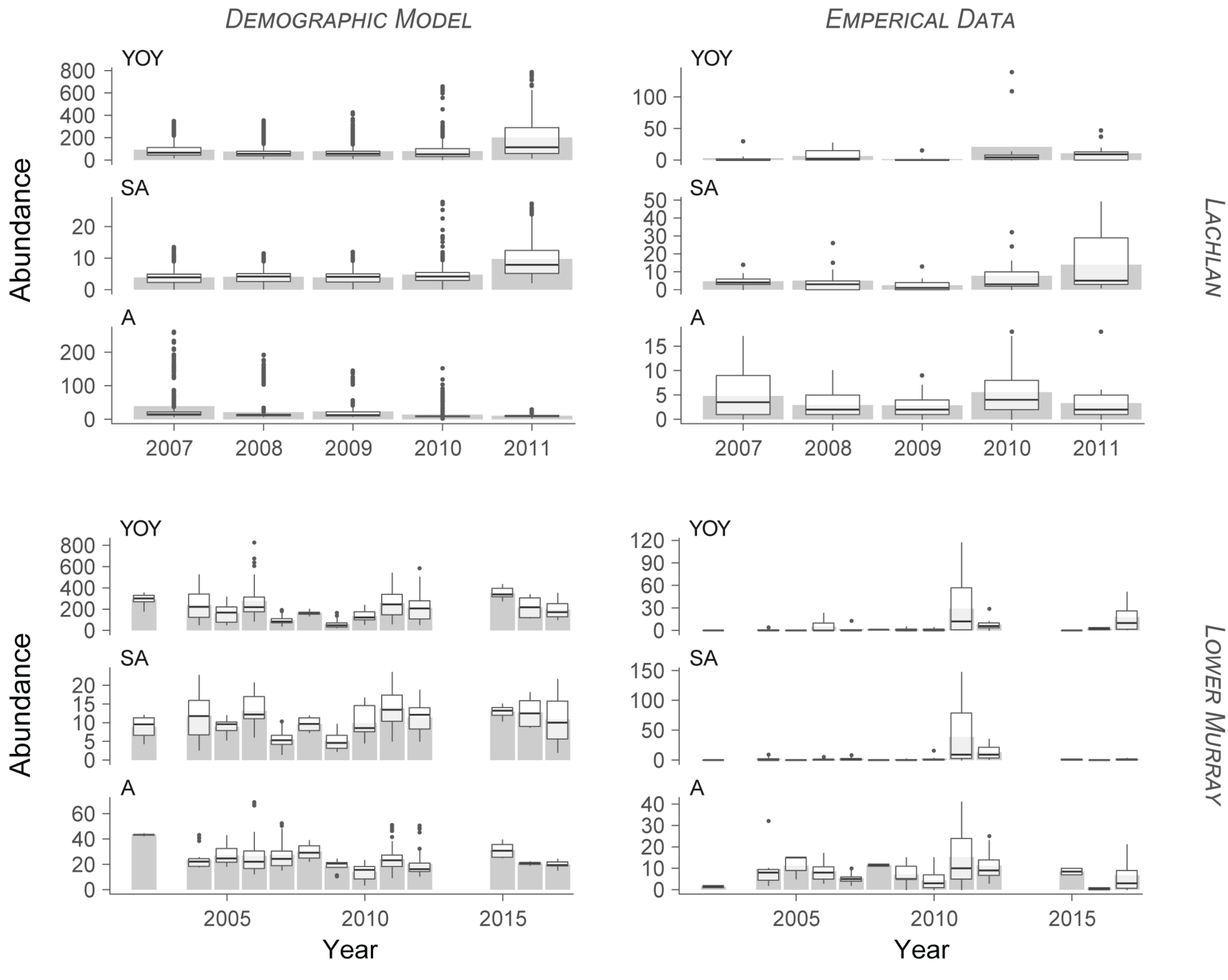
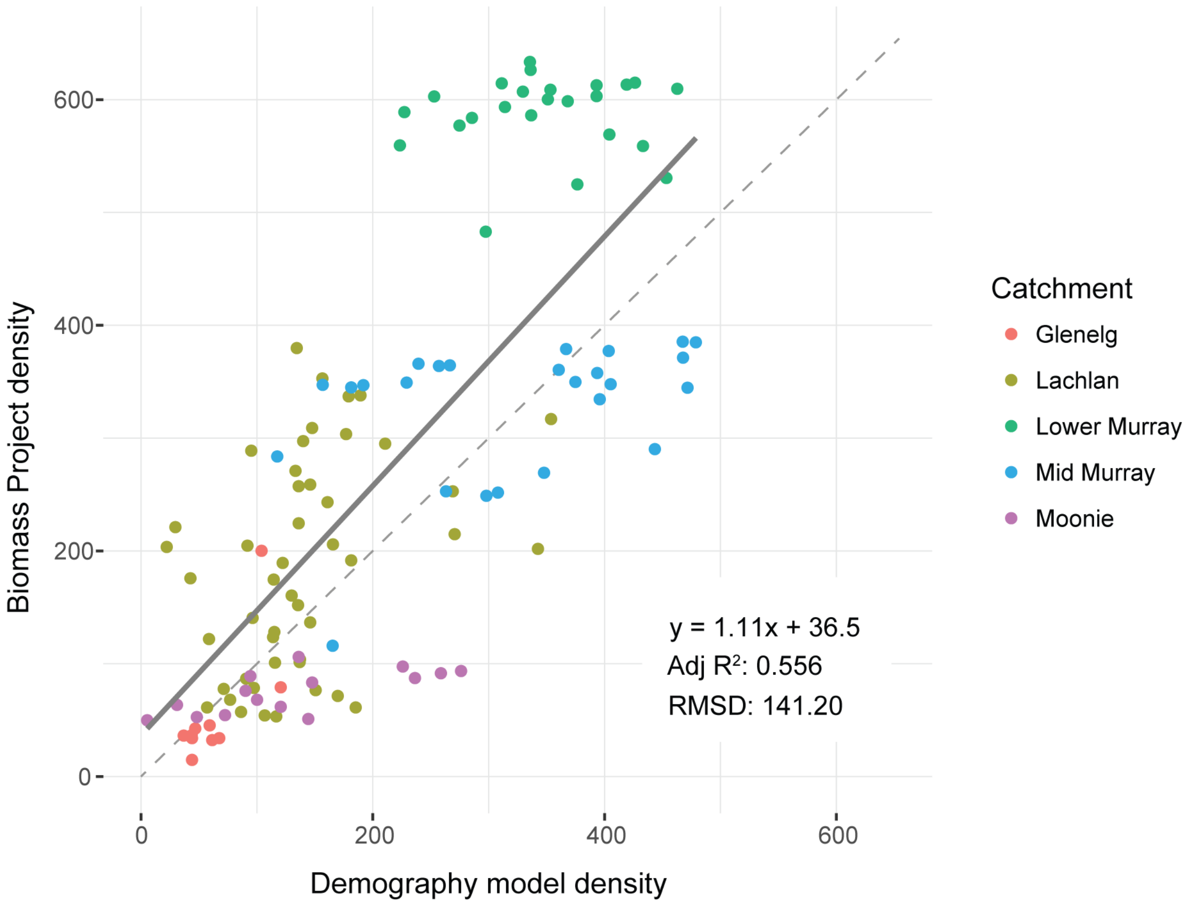


Figure 3.13

Comparison of the biomass density values (kg.ha^{-1}) for intersection regions at the habitat mosaic/sub-population scale, between the demography model and the Biomass Project. Grey solid line indicates the linear regression fit (fitted to all catchments simultaneously) and dashed line is one-to-one relationship. The linear model equation and associated adjusted R^2 (Adj R^2), and the root mean square deviation (RSMD) is also provided. Note that the slope (1.11) and intercept (36.5) of the linear regression do not significantly differ from 1 ($p = 0.242$) and 0 ($p = 0.104$), respectively.



Supplementary Material

S1 Dispersal Kernel Development

Background

To inform movement in our demography model, we developed a movement kernel based on empirical data on carp movement in the Murray-Darling Basin. Here we focus on the longitudinal movement of carp between subpopulations along a connected river system using two different carp movement data sets. Lateral movement into specific habitats such as floodplain wetlands is not the designated purpose of this model.

Data sets

We explore two data sets for the development of a statistical carp dispersal kernel. The first was a carp movement study in the mid-Murray by Stuart and Jones (2006b). This study used mark-recapture and radio-telemetry to investigate the movement and dispersal patterns of carp in a large lowland river system from 1999 to 2001. All carp were captured at a single location, Barmah-Millewa forest, and dispersal distance calculated based upon recapture location and the distance along the river network. In this study 8.8% of the marked carp were recaptured by either electro-fishing surveys, recreational anglers, a commercial fishery at Moira Lake, or by weir keepers at Torrumbarry fishway (Stuart and Jones 2006).

The second data set was FishNet (https://pit-tags.com.au/FishNet) with data downloaded 1/3/2019. The data used from FishNet was commissioned by the Murray Darling Basin Authority and contains carp movement data derived from PIT tagged fish moving through a network of detectors. Many of the detectors are located on fishways and locks throughout the Murray River and used to monitor the movement of a range of fish species, of which carp is one. Within the analysed dataset, 3110 unique carp tags were detected within the system representing only a fraction of the total tagged fish released into the river network. Of these detected tags, 1116 were recorded as making a transition through the network past one reader to another. The minimum total distance based upon the sequence of detections across multiple transmitters is used in this analysis which considers the timing and location of all detections across the network not just the first and last detections.

Analysis

We undertook analysis in R, using the 'fitdistrplus' and 'MASS' packages. Using distances moved, we fitted data to several candidate distributions including normal, log-normal, gamma, Weibull and exponential distributions. Goodness of fit between observed and candidate distributions was considered using Kolmogorov-Smirnov and Cramer-von Mises statistics, as well as Akaike's Information criterion and Bayesian Information Criterion. The resulting kernels considered the proportion of individuals moving as a fraction of the total detections occurring within the data set. We based the development of movement kernels was on the composite of the largest distance moved along the river network by each fish, which for the FishNet data was based upon movement between multiple detectors and for Stuart and Jones (2006) was distance from capture to re-capture.

Results

The best fit model was the log-normal distribution, which has the form:

$$\frac{1}{\sqrt{2\pi}\,\sigma x}\exp[-\frac{1}{2\sigma}\,(\ln(x)-\mu)^2\,].$$

plnorm($\boldsymbol{x}$, $\boldsymbol{\mu}$ and $\boldsymbol{\sigma}$) returns the cumulative probability distribution for the value of $\boldsymbol{x}$ and is implemented in R with the following model and parameters:

(plnorm($\boldsymbol{x}^{max}$,meanlog=fit[1],sdlog=fit[2])-plnorm($\boldsymbol{x}^{min}$,meanlog=fit[1],sdlog=fit[2])) * $\boldsymbol{d}$ * $\boldsymbol{p}$

where: $\boldsymbol{x}^{max}$ is a theoretical maximum dispersal distance (e.g. length of the Basin)

$\boldsymbol{x}^{min}$ is the dispersal distance between the two locations of interest

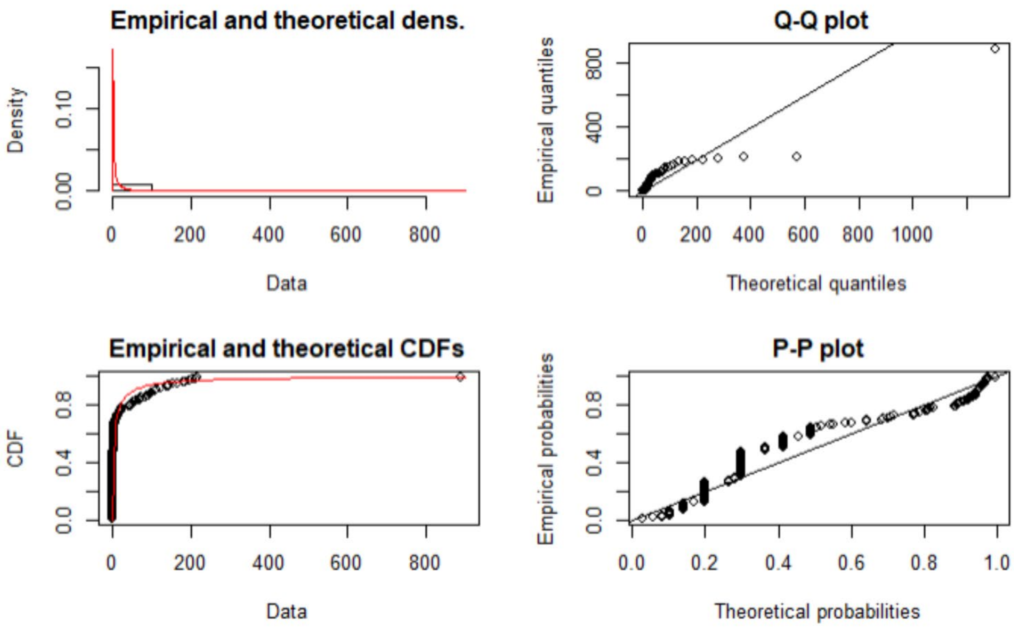
$\boldsymbol{d}$ is the fractional proportion of the individuals that are non-stationary

$\boldsymbol{p}$ is the size of the source population

Although the movement model was fitted to both data sets, we only used the model fitted to the Stuart and Jones (2006) data in the main text. This is because the FishNet data underestimated movement at small distances (<30km) due to minimum distances between fishways, which were typically located at weirs, dams etc..

Figure S1

Fit between observed data and the cumulative distribution function of the best fitting log normal distribution for the Stuart and Jones (2006) and the FishNet data,



respectively.

Table S1

Goodness-of-fit statistics for both the Stuart and Jones (2006b) and FishNet movement datasets. Smaller values signify improved fit properties between the modelled distribution and the observed data

Test statistic	Stuart & Jones (2006)	FishNet
Kolmogorov-Smirnov statistic	0.1800	0.0827
Cramer-von Mises statistic	1.1598	1.1717
Akaike's Information Criterion	1196.76	14061.87
Bayesian Information Criterion	1203.13	14071.90

Supplementary Tables

Table S2

Date ranges and model run times (weeks) for the demographic model for the five study catchments.

Catchment	Start Date	End Date	Run time
Lachlan	03-07-2000	05-12-2016	855
Lower Murray	01-07-1991	04-12-2017	1372
Mid Murray	01-07-1991	06-04-2018	1389
Glenelg	01-07-1991	06-04-2018	1389
Moonie	02-07-1990	08-06-2015	1295

Supplementary Figures

Figure S2

Conceptual diagram of the network analysis and community detection process for delineating metapopulations for each study catchment.

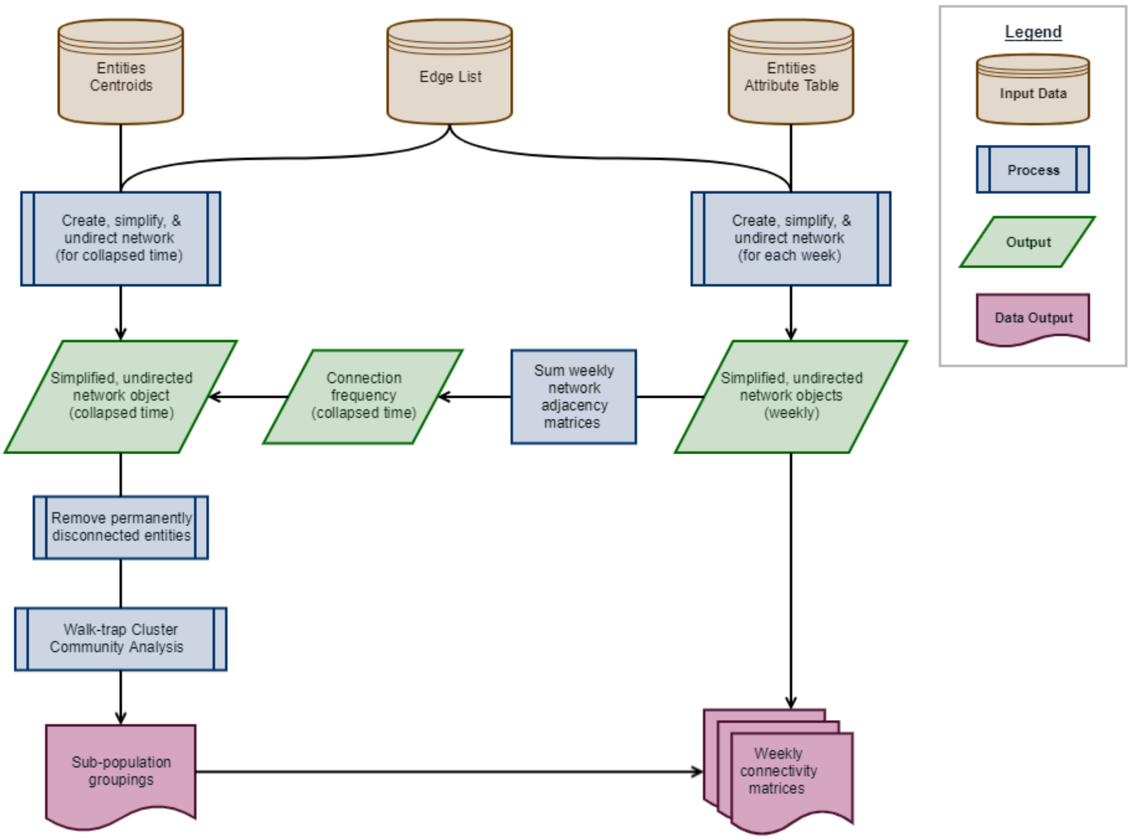


Figure S3

Number of network edges that existed (i.e. two entities were connected) during the study period in the Moonie River catchment.

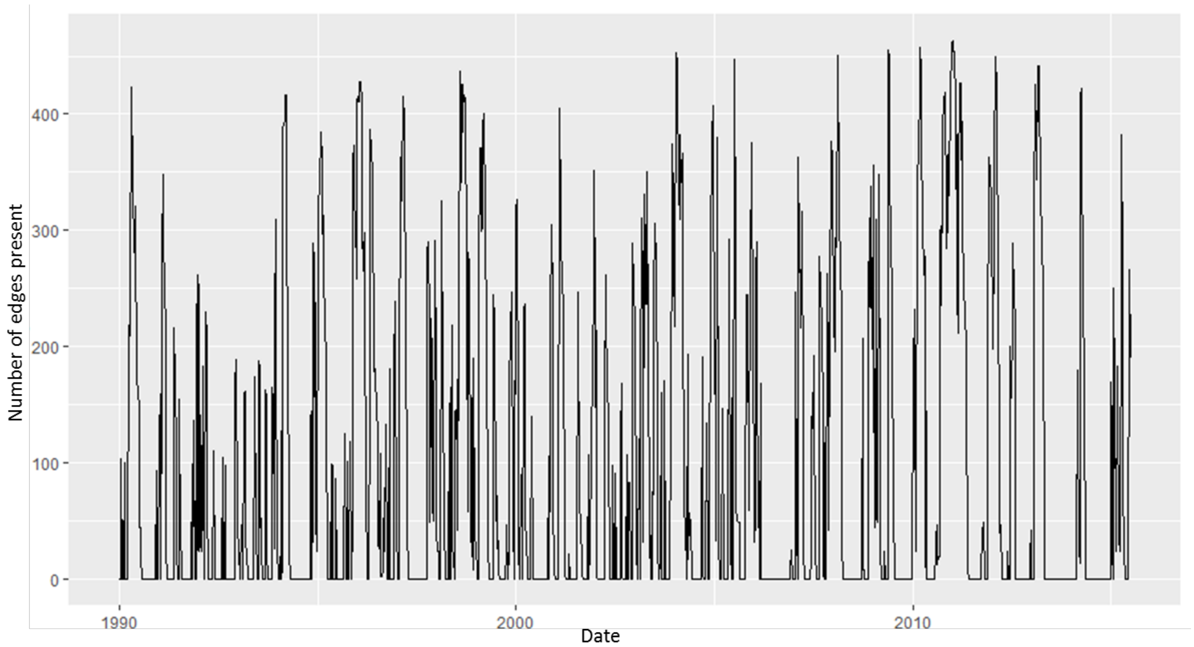


Figure S4

Breakdown of connectivity of network edges (i.e. whether a biologically relevant connection exists between water bodies) over time in the Moonie River catchment. Blue indicates when two entities were connected (i.e. the edge existed). Each row is a unique edge between two notes.

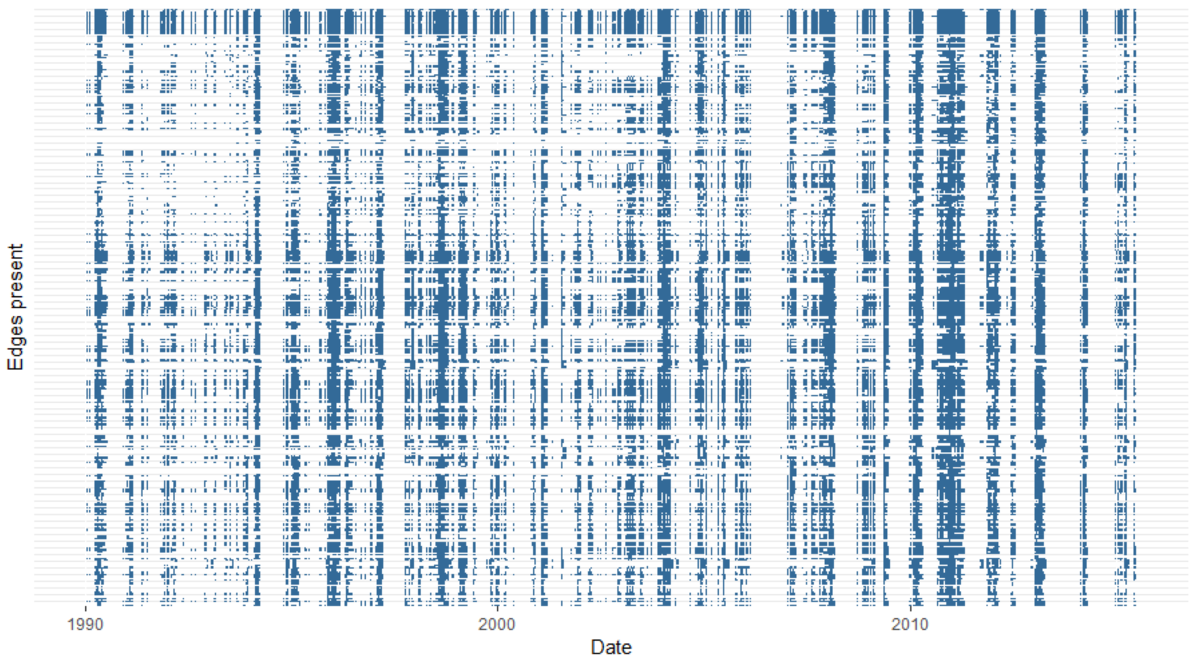


Figure S5

Number of network edges that existed (i.e. two entities were connected) during the study period in the Lachlan River catchment.

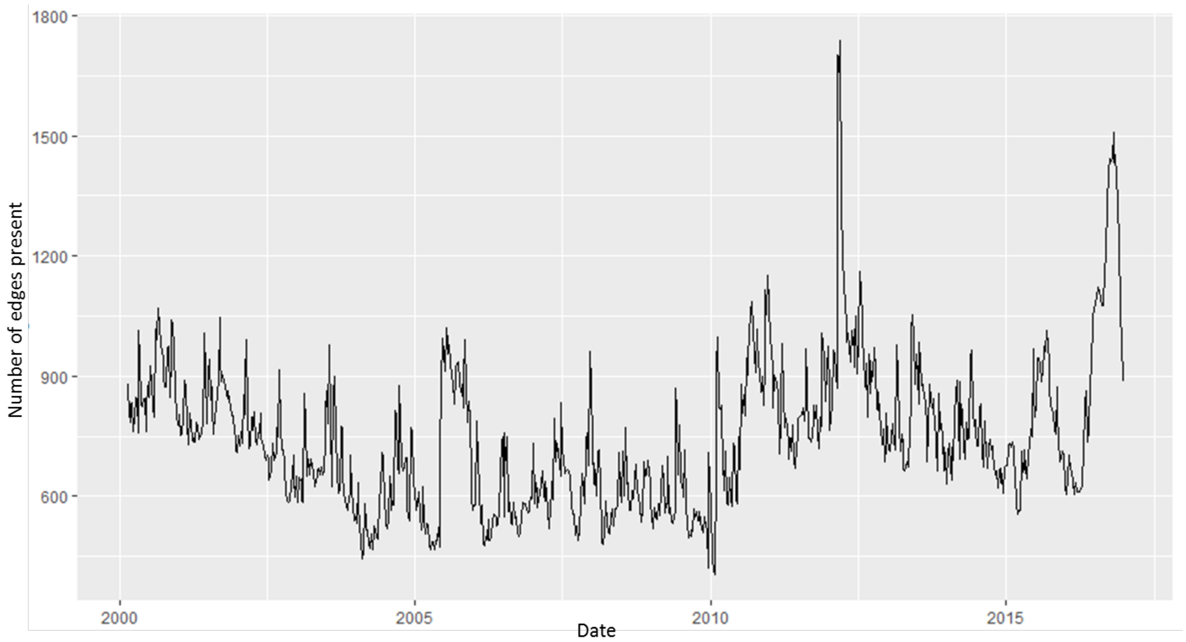


Figure S6

Breakdown of connectivity of network edges (i.e. whether a biologically relevant connection exists between water bodies) over time in the Lachlan River catchment. Blue indicates when two entities were connected (i.e. the edge existed). Each row is a unique edge between two notes.

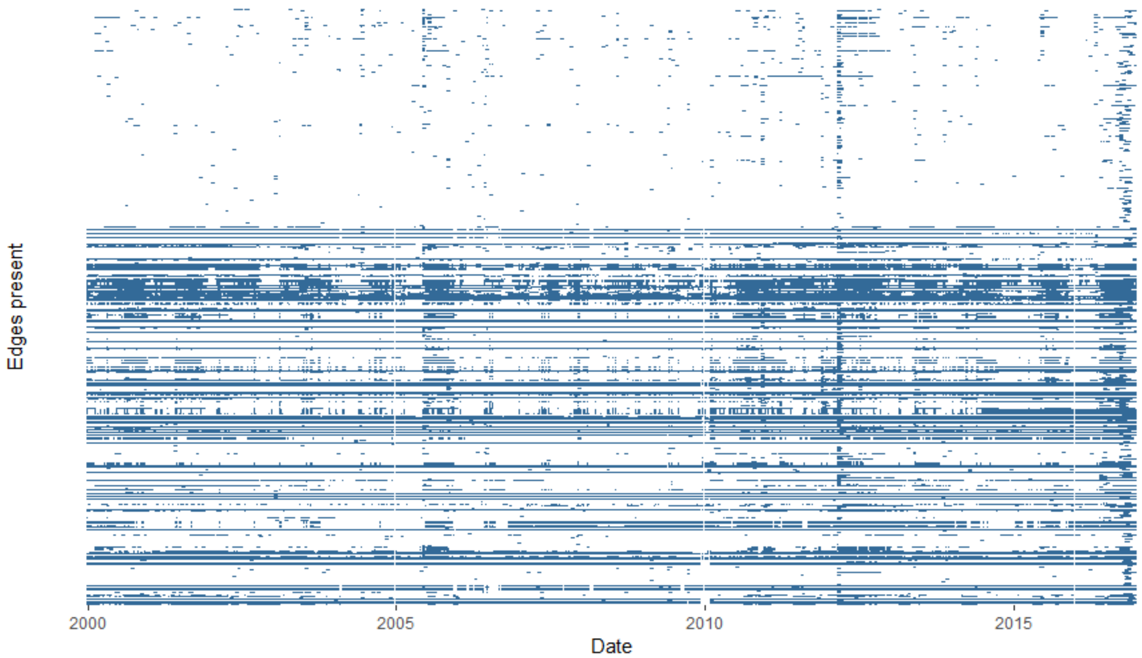


Figure S7

Number of network edges that existed (i.e. two entities were connected) during the study period in the Mid Murray River catchment.

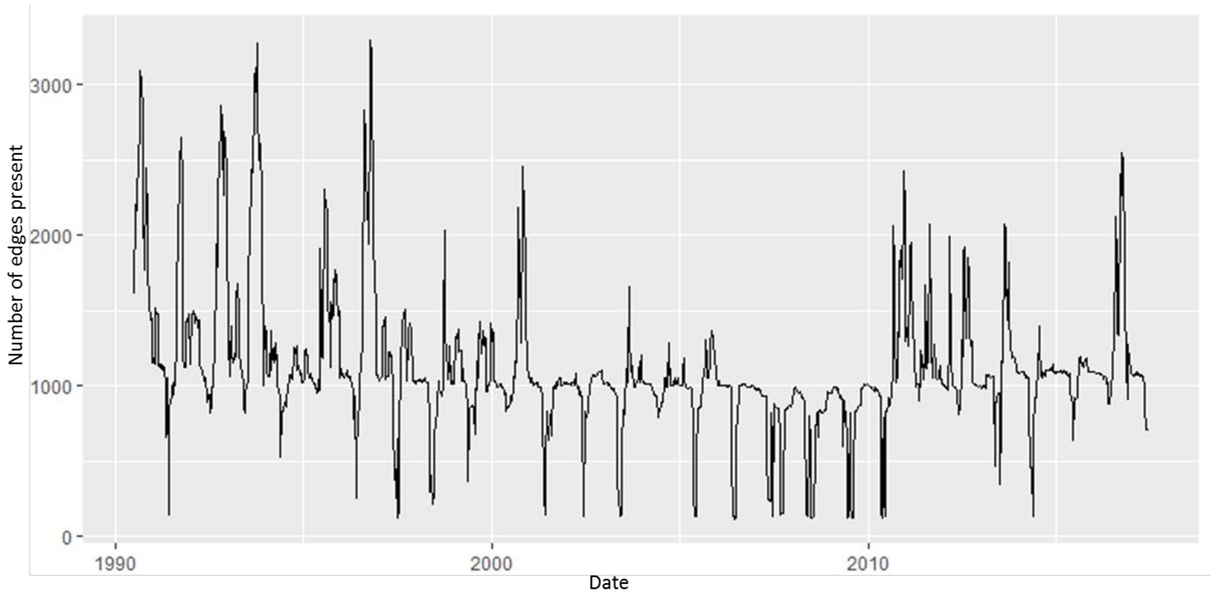


Figure S8

Breakdown of connectivity of network edges (i.e. whether a biologically relevant connection exists between water bodies) over time in the Mid Murray River catchment. Blue indicates when two entities were connected (i.e. the edge existed). Each row is a unique edge between two notes.

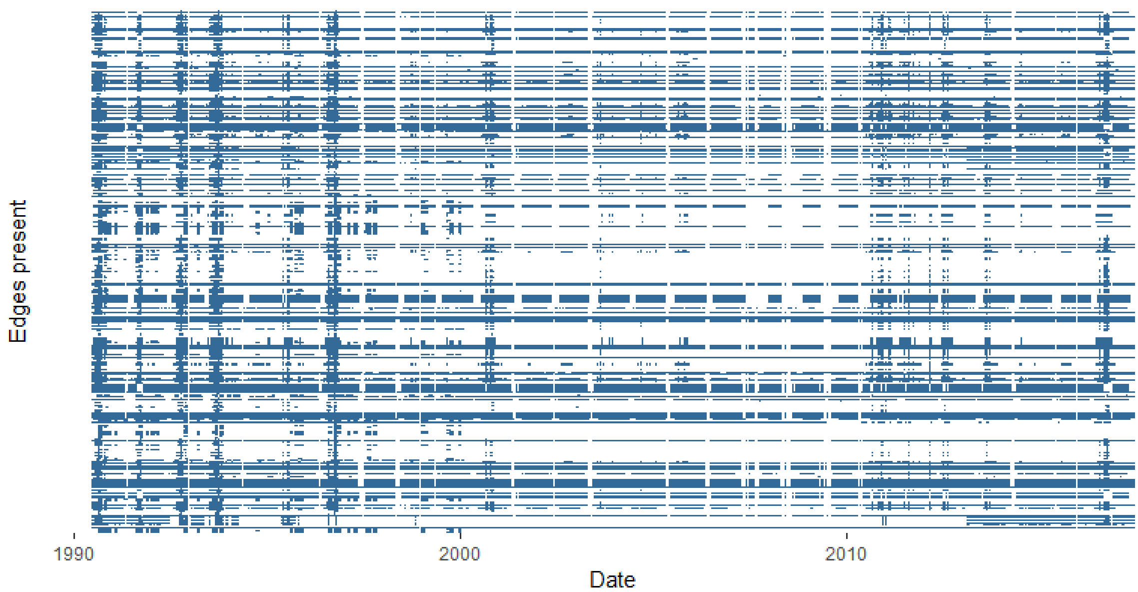


Figure S9

Number of network edges that existed (i.e. two entities were connected) during the study period in the Lower Murray River catchment.

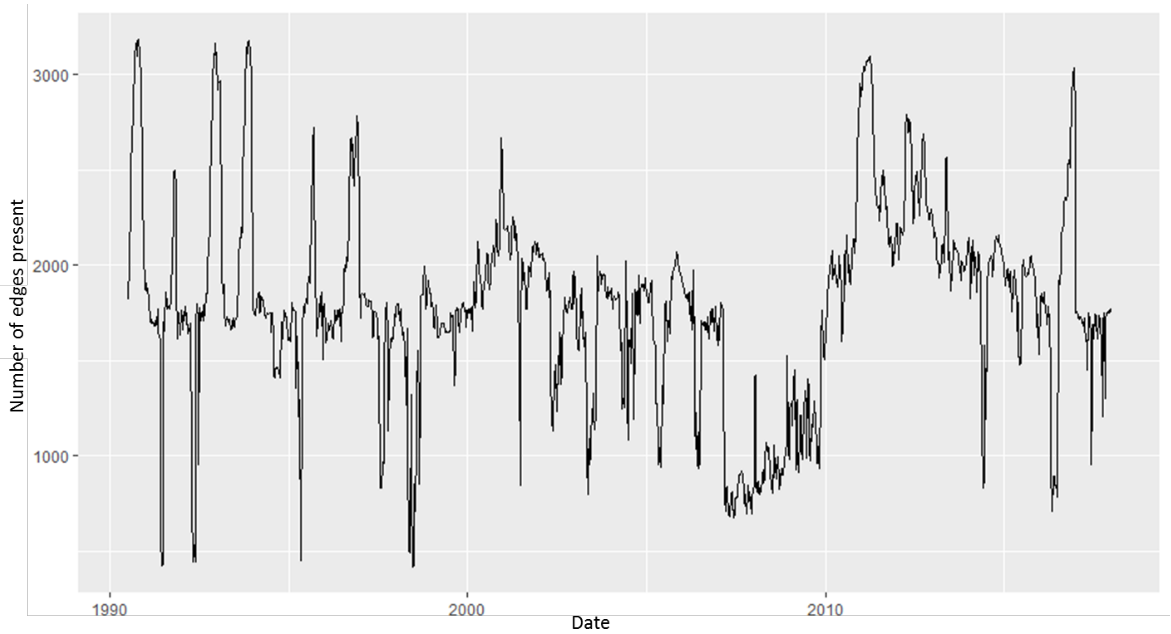


Figure S10

Breakdown of connectivity of network edges (i.e. whether a biologically relevant connection exists between water bodies) over time in the Lower Murray River catchment. Blue indicates when two entities were connected (i.e. the edge existed). Each row is a unique edge between two notes.

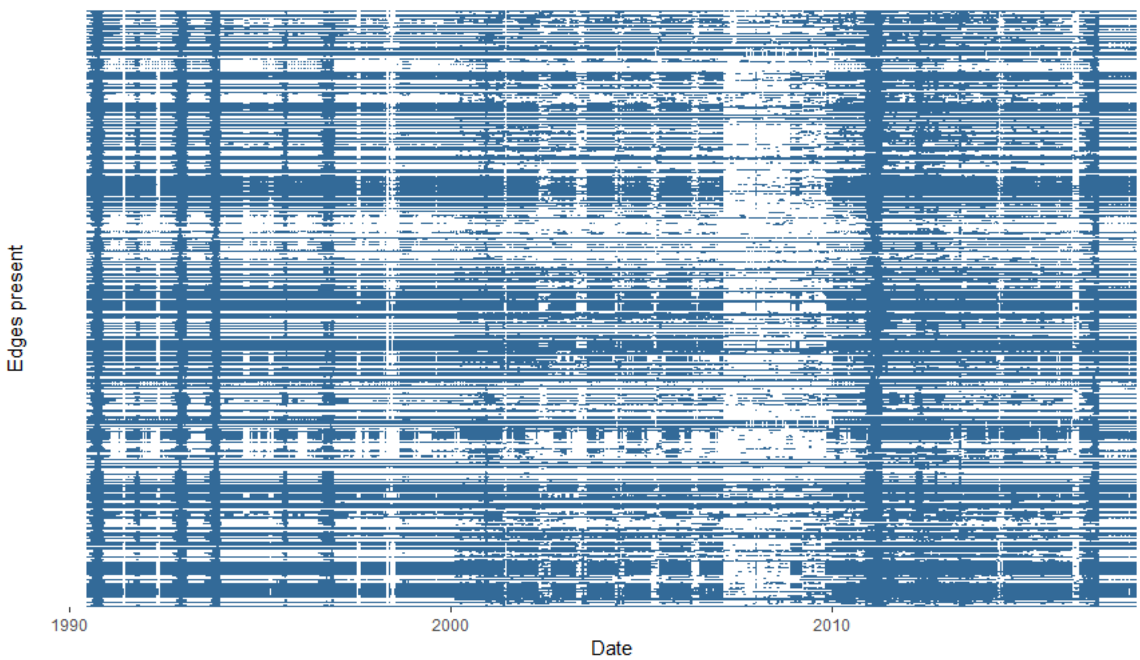


Figure S11

Number of network edges that existed (i.e. two entities were connected) during the study period in the Glenelg River catchment.

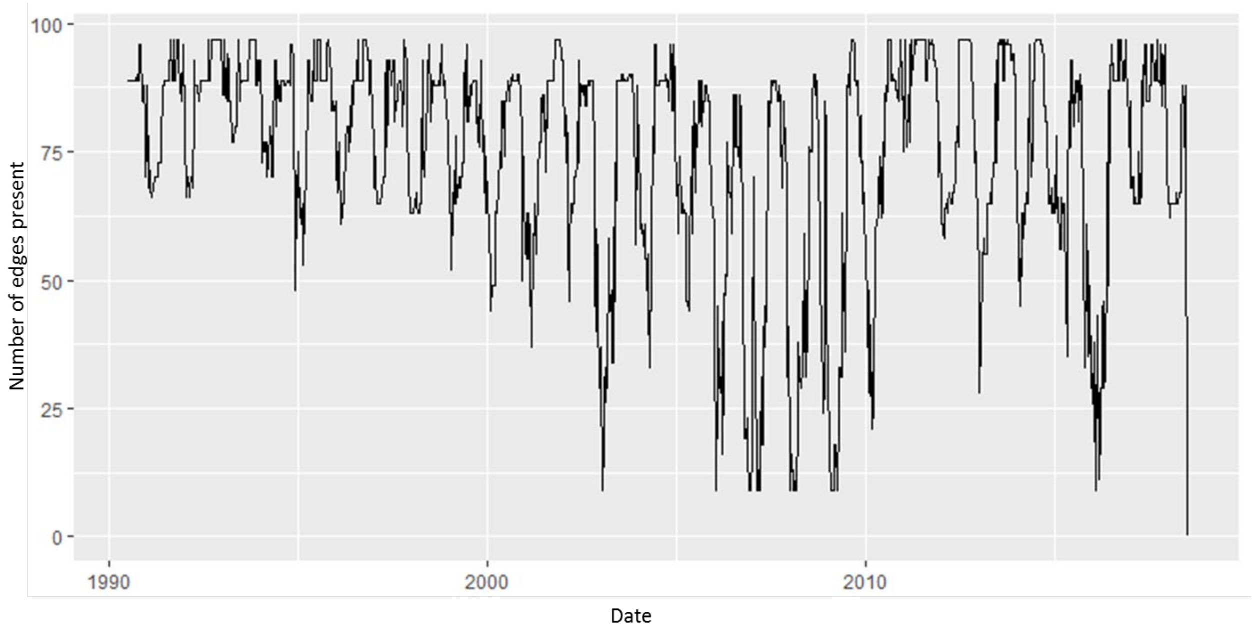


Figure S12

Breakdown of connectivity of network edges (i.e. whether a biologically relevant connection exists between water bodies) over time in the Glenelg River catchment. Blue indicates when two entities were connected (i.e. the edge existed). Each row is a unique edge between two notes.

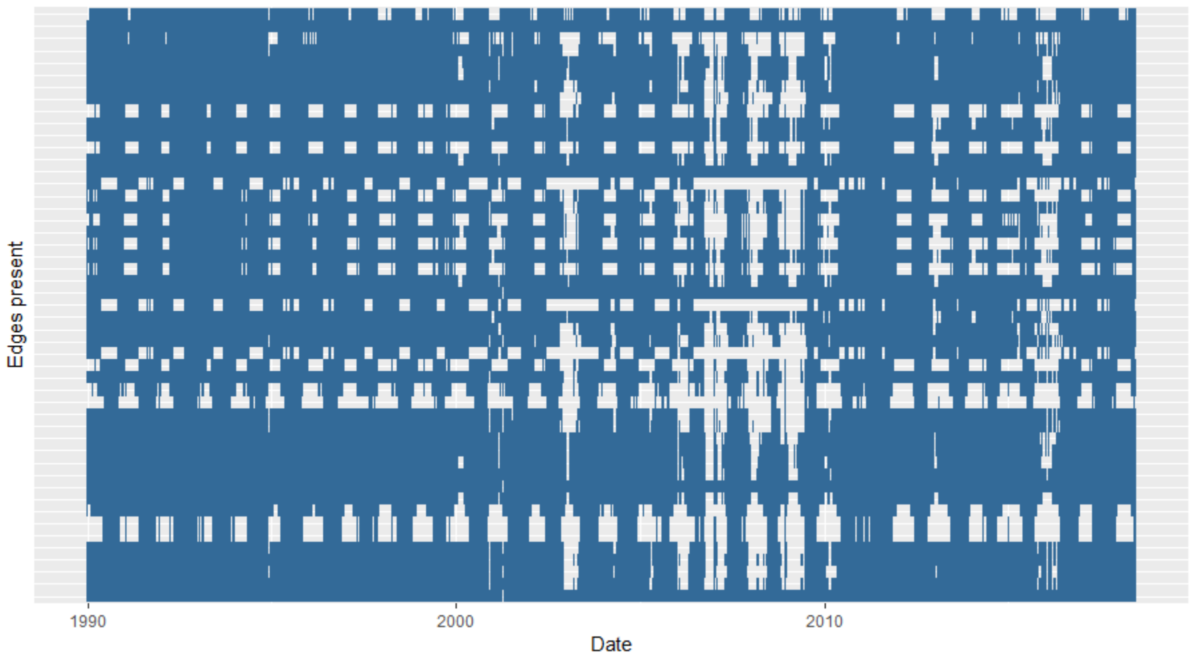


Figure S13

Proportion of habitat in each catchment that was suitable for spawning aggregations (as per the habitat suitability modelling, SECTION 2). Colours indicate years in which there was suitable habitat for spawning aggregations.

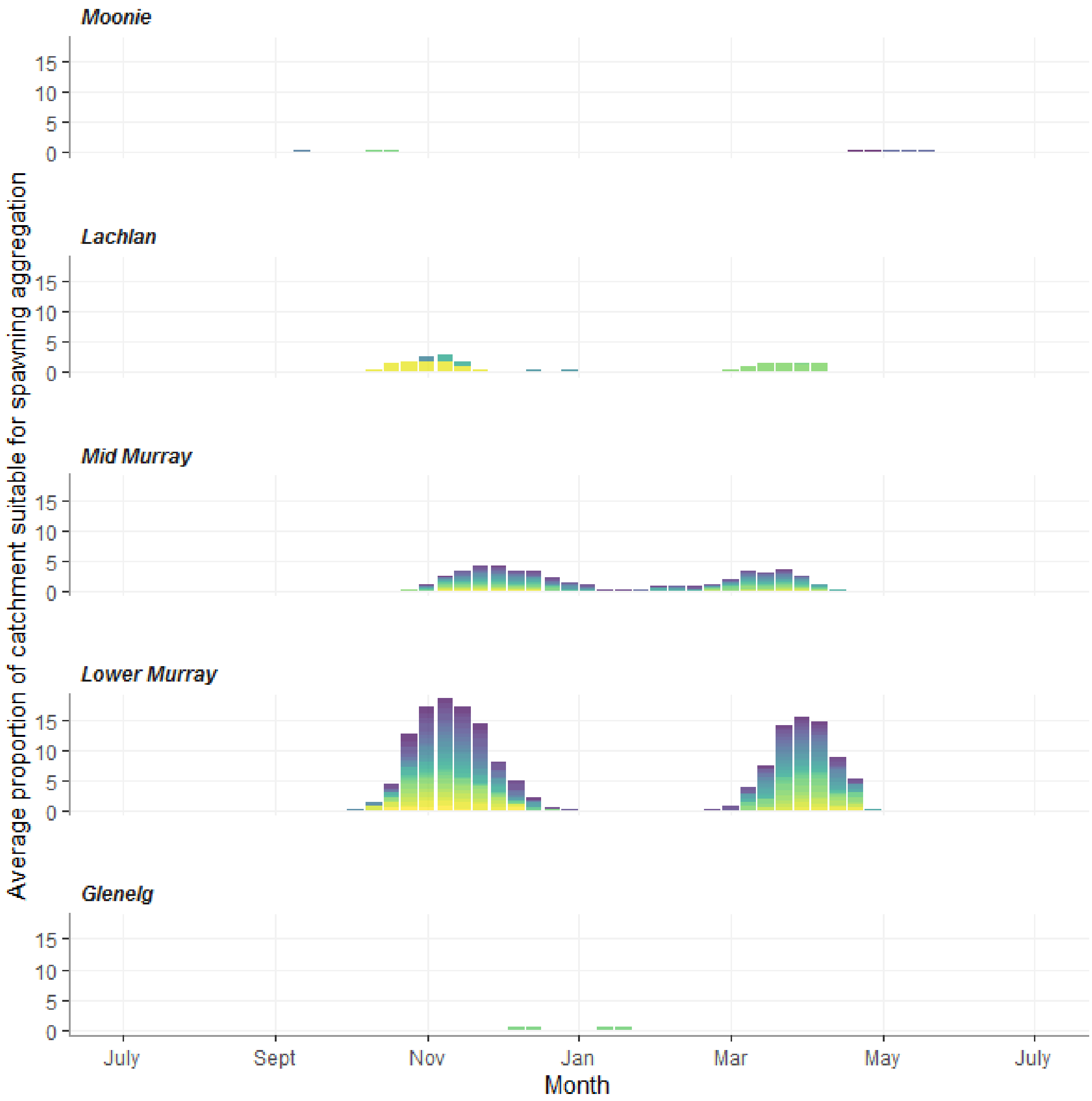


Figure S14

Distribution function for the production of eggs over the year.

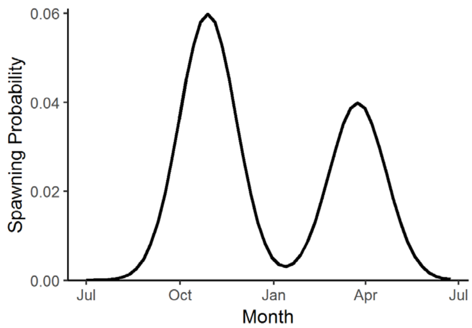


Figure S15

Area of grouped habitat types (colours) in the defined sub-populations of the Lachlan River catchment. Bold number indicate sub-population number, with numbers in parenthesis indicating neighbouring subpopulations.

Figure S16

Area of grouped habitat types (colours) in the defined sub-populations of the Moonie River catchment. Bold number indicate sub-population number, with numbers in parenthesis indicating neighbouring subpopulations.

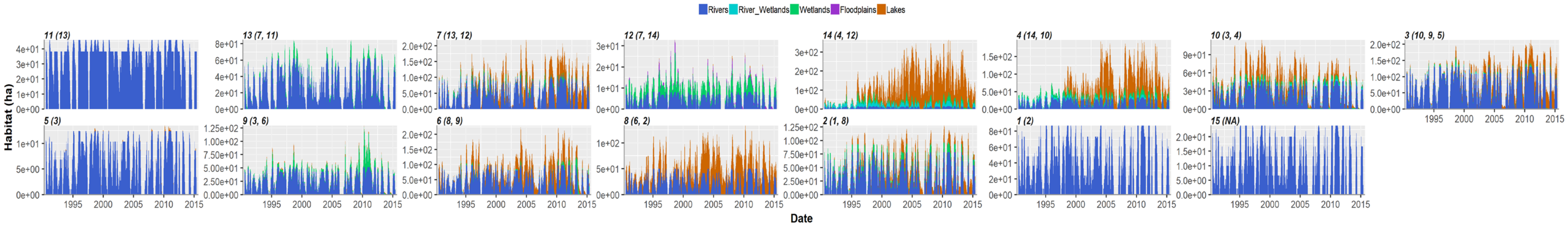


Figure S17

Area of grouped habitat types (colours) in the defined sub-populations of the Mid Murray River study area. Bold number indicate sub-population number, with numbers in parenthesis indicating neighbouring subpopulations.

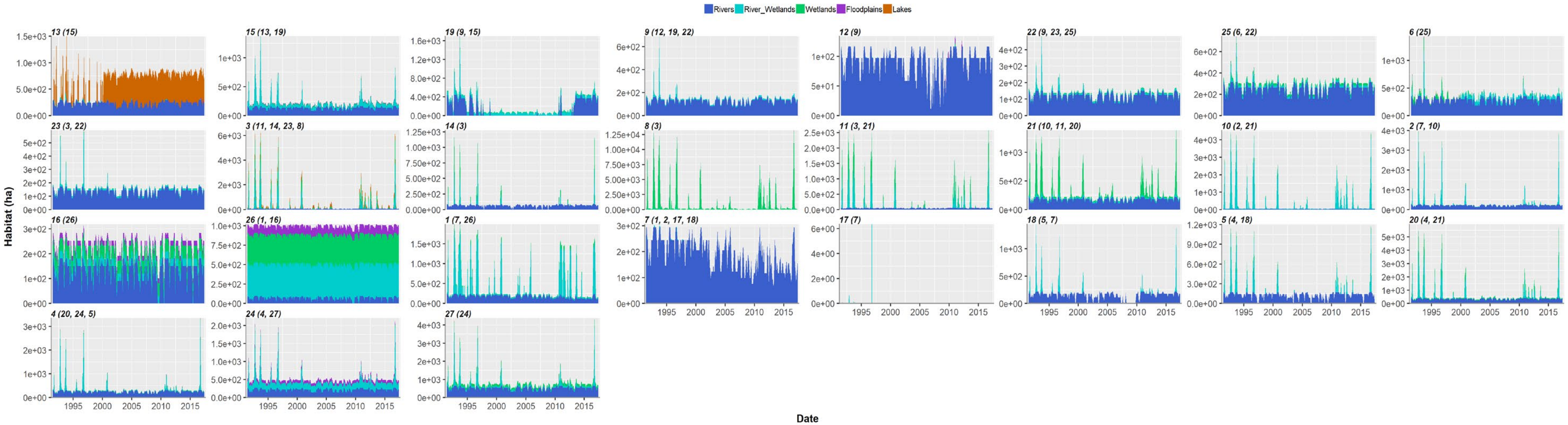


Figure S18

Area of grouped habitat types (colours) in the defined sub-populations of the Lower Murray River study area. Bold number indicate sub-population number, with numbers in parenthesis indicating neighbouring subpopulations.

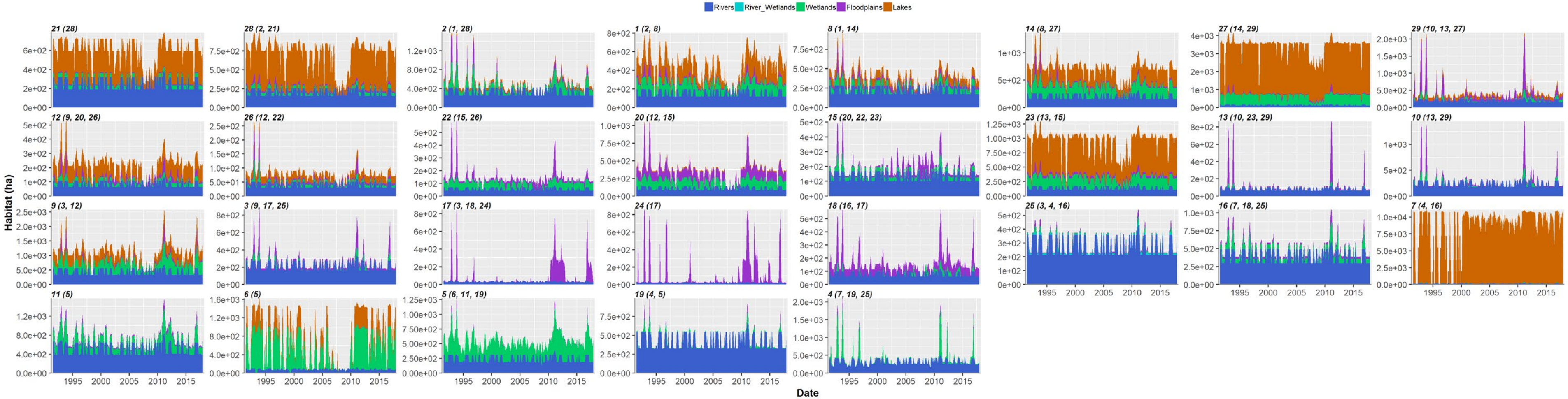


Figure S19

Area of grouped habitat types (colours) in the defined sub-populations of the Glenelg River catchment. Bold number indicate sub-population number, with numbers in parenthesis indicating neighbouring subpopulations

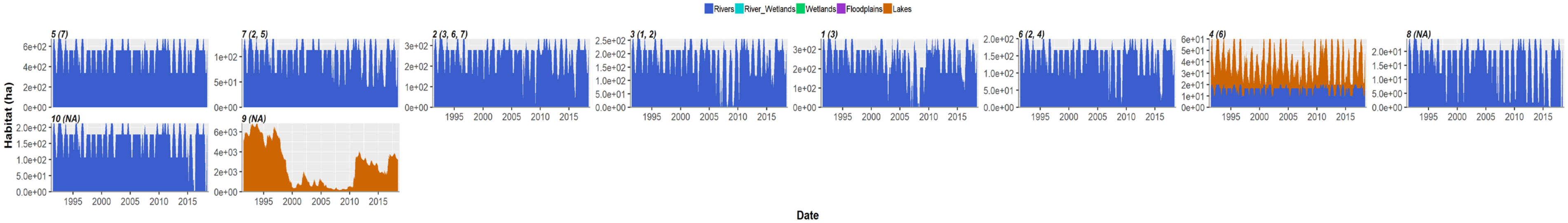


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Figure S20

Sensitivity of time (in years) to 50, 70, and 90% recovery, after an 80% knockdown, to changes in the overall strength of density dependence across the five study catchments. Here both the strength of larvae and young-of-year density dependence (c_1) and the strength of sub-adult density dependence (c_2) are halved (low) or doubled (high) compared to the baseline (medium c_1 and c_2), reflecting scenarios where carp abundances are either, on average, greater or less, respectively, than those predicted by the habitat suitability model. Summary statistics for the box and whisker plots are the median and the first and third quartiles (the 25th and 75th percentiles; the lower and upper hinges).

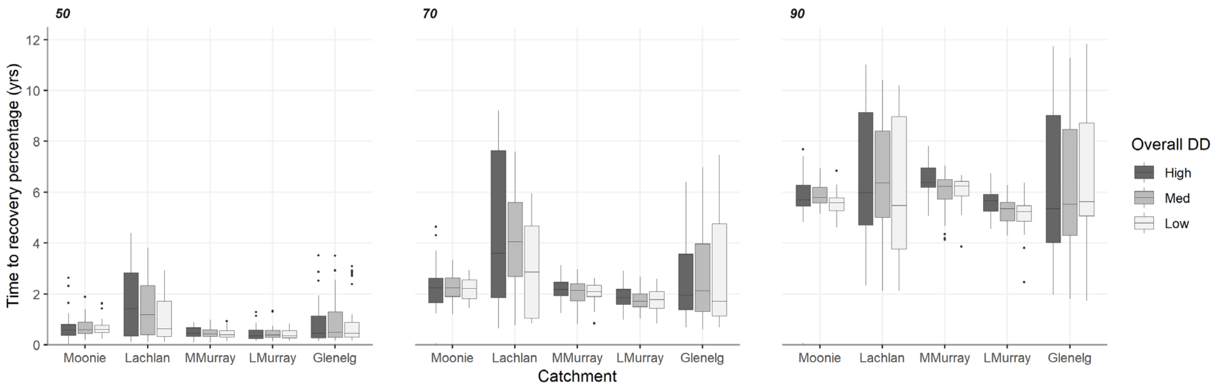
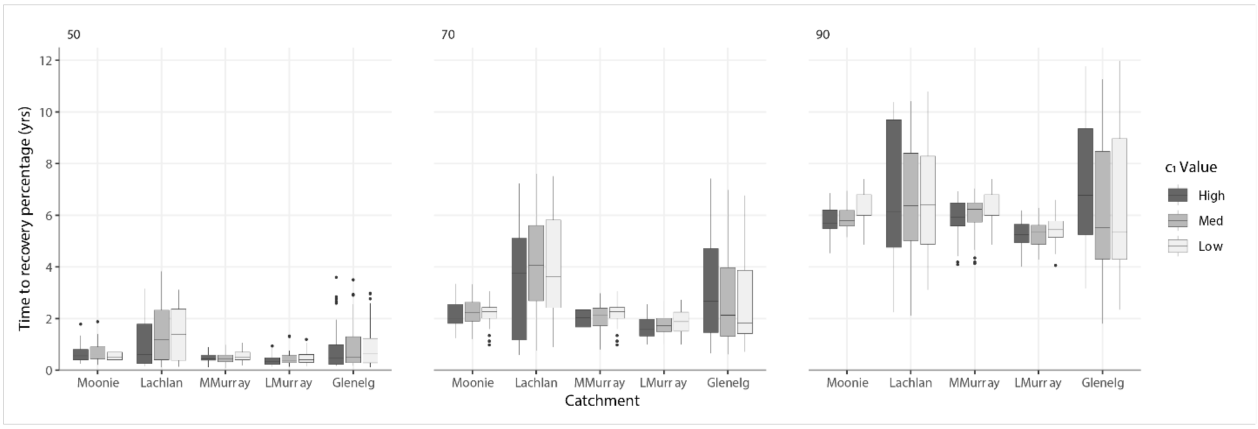


Figure S21

Sensitivity of time (in years) to 50, 70, and 90% recovery, after an 80% knockdown, to changes in the strength of larvae and young-of-year strength of density dependence (c_1) across the five study catchments. Here the c_1 is halved (low) and doubled (high) and the strength of density dependence for sub-adults (c_2) is inversely co-varied (i.e. increased and decreased, respectively) such that the abundance time-series follows that of the baseline scenario (medium c_1 and c_2). Summary statistics for the box and whisker plots are the median and the first and third quartiles (the 25th and 75th percentiles; the lower and upper hinges).



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SECTION 4 – Epidemiological Modelling

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Abstract

Common carp (*Cyprinus carpio*) now dominate much of the Murray-Darling Basin in South-eastern Australia and are implicated in the degradation of Australia's waterways. The need to reduce carp abundance has led the Australian government to fund research into Cyprinid herpesvirus 3 (CyHV-3) as a possible biocontrol agent, with the intention to release within the next 5 years. Building on a series of integrated hydrological, habitat suitability, and demographic models, we developed an epidemiological model and applied this to five representative catchments in southeastern Australia to predict the impact of releasing CyHV-3 on carp abundance. The dynamics of transmission and infection were captured by a set of differential equations embedded in a discrete demographic metapopulation model wherein ageing, movement, natural mortality and recruitment of carp occurred on a weekly time-scale. To study the potential of the virus under realistic population dynamics the model was run using historical time series of hydrological conditions recorded from the mid-1990s to the end of 2016 as available for each of the five catchments. These time series include the dramatic fluctuations in flows and conditions associated with the Millennial Drought and its ending that affected much of Australia. Whether CyHV-3 caused a meaningful reduction in carp abundance critically depended on whether seasonal reactivation of the virus, and onward infection, occurs in chronically infected carp. In the absence of reactivation, the virus was predicted to cause a single mortality event from which carp populations rapidly recovered. When reactivation was allowed, the model predicted similar initial mortalities but also sustained reductions in carp abundance driven by seasonal outbreaks mostly amongst immature carp. The subsequent outbreaks were predicted to be at least an order of magnitude smaller than the initial outbreak following release. With seasonal reactivation and favourable contact rates the model results were insensitive to the frequency that reactivation occurs and the year of release, with suppression of carp abundance consistently being 50-70% of that expected if there was no virus. The results were sensitive to the survival rate of carp following first infection with CyHV-3 underlining the importance that Australian carp are naïve to the virus release. The simulations also showed that this knock-down would be sufficient to reduce catchment level populations for at least 10 years below an estimated damage threshold of 100 kg/ha in many reaches and waterbodies. However, in the particularly high-density areas of the Murray River, complementary measures, particularly commercial fishing, would be recommended to reduce population density before virus release.

Keywords

Mathematical model, epidemiological model, *Cyprinus carpio,* density-dependent transmission, frequency-dependent transmission, SIR model

Introduction

Invasive vertebrates are a major threat to biodiversity and conservation in many ecosystems. For freshwater systems, a major invasive species is the common carp (*Cyprinus carpio*) which has been introduced into river and lake systems in many parts of the globe and has become a serious problem in North America and Australasia (Hicks and Ling, 2015). Whilst there were several attempts at the introduction of carp into Australia, it was not until the early 1960s when the "Boolarra" strain was imported into eastern Victoria did the species become a serious invasive vertebrate pest species (Shearer and Mulley, 1978). Within 10-15 years it had spread to large parts of the Murray Darling Basin (MDB) and by the 1990s was increasingly recognised as one of the most serious ecological threats to the basin (Koehn, 2004). This is in part due to its high rate of intrinsic population growth, but also due to its benthic feeding which can lead to turbidity of waterways, making them less suitable for native fish with a requirement for conditions of high sunlight penetration (Forsyth et al., 2013; Roberts et al., 1995; Weber and Brown, 2009). Nevertheless, there is an ongoing debate as to the extent to which the dominance of carp (and the associated decline in native fish in the MDB is a consequence of river management rather than its cause (Gehrke et al., 1995; Gehrke et al., 2011; Nicol et al., 2004).

Following the recognition of carp as a serious threat to the health of the Murray Darling Basin, strategies for control have been researched (Brown and Gilligan, 2014; Brown and Walker, 2004; Roberts and Tilzey, 1997)). The high fecundity of the species and its invasive capabilities tend to lead to the conclusion that intensive fishing alone is unlikely to achieve sustainable control (Brown and Gilligan, 2014; Thresher, 1997). This led to the exploration of a novel method of genetic control, which relies on the release of genetically modified adults carrying a recombinant construct which causes female-specific lethality and thus a gradual population collapse (Bax and Thresher, 2009; Thresher et al., 2014b). Whilst it has been possible to implement this "daughterless" technology in carp, modelling studies showed that to be effective in the short-medium term, it would need to be combined with a complementary control approach (Thresher et al., 2014a).

One potential complementary approach is the use of an infectious disease agent, of which a leading candidate is Cyprinid herpes virus 3 (CyHV-3) (McColl et al., 2014). CyHV-3 was first recognised in Germany as a serious pathogen of carp in 1997 (Bretzinger et al., 1999), and thereafter caused extensive epidemics in Asia (Pearson, 2004), including Indonesia (Sunarto et al., 2011). The virus did not reach Australia, but soon after, in recognition of the potential of the virus as a biocontrol agent, a research program was initiated to determine through infection trials if it possesses virulence for strains of carp present in the MDB. Following this confirmation (Sunarto et al., 2014) non-target species testing was undertaken against a wide range of aquatic species found in the waterways of south-eastern Australia, which demonstrated that none of them became infected (McColl et al., 2017).

Based on these results demonstrating the potential of CyHV-3 as a biocontrol agent, the logical next step is to inform a virus "release strategy". By this, we mean where, when and how best to release the virus to achieve a maximum impact on reducing the carp population, both in the immediate and long-term. At the same time, there is a need to minimise the potential of adverse consequences, particularly the effect of mass mortality events (and the subsequent decomposition) inducing water anoxia (Lighten and van Oosterhout, 2017).

Due to its importance to aquaculture, the fundamental transmission dynamics of CyHV-3 are relatively well studied (Boutier et al., 2015). There is a consensus on the importance of a permissive temperature range – approximately between 16 and 28 °C - within which infection progresses to disease, viral excretion and onward transmission (Yuasa et al., 2008). Within this permissive range, there is very high mortality in naïve fish (>80%) with a peak of mortality between approximately 8 and 12 days post infection (Perelberg et al., 2003). Experimentally, the skin has been shown to be a major portal of entry of the virus (Costes et al., 2009) and as the virus does not survive more than a few days in water at temperatures in the permissive range (Perelberg et al., 2003), indirect transmission is considered to be much less important than direct transmission. In wild populations, a strong seasonal pattern has been shown in both Japan (Uchii et al., 2011) and North America (Thresher et al., 2018), which is considered to be driven by a combination of warming water entering the permissive temperature range and enhanced skin-to-skin contact during behavioural aggregation (Uchii et al., 2014; Uchii et al., 2011).

There is however more uncertainty regarding host-pathogen interactions, especially regarding immunity and viral persistence in fish which recover from infection. In particular, while there is considerable evidence that CyHV-3 can undergo latency in recovered fish - whereby its viral DNA persists in certain cells as circular episomes – this is yet to be proved conclusively (Boutier et al., 2015). Similarly, it is uncertain under which conditions reactivation occurs and how important is stress in facilitating this (Lin et al., 2017) and to what extent reactivation always leads to a recrudescent disease state and onward transmission (Bergmann and Kempter, 2011). There is also some disagreement in the literature regarding the susceptibility of carp larvae to infection as while Ito et al. (2007) showed that early stage larvae were "not susceptible" to disease, Ronsmans et al. (2014) demonstrated that carp are sensitive and permissive to CyHV-3 infection at all stages of development.

Despite there being a relatively good understanding of the principles of transmission of CyHV-3, there is nevertheless an absence of quantified parameters, such as the transmission rate ("beta") and the basic reproductive number ("R_0"), and accordingly few CyHV-3 published models. Taylor et al. (2011) presented a simple model of the spread of koi herpesvirus disease in England and Wales but used infected sites (or fisheries) rather than individual fish as the modelled unit. A somewhat more relevant study was by Omori and Adams (2011) who modelled the seasonal dynamics of outbreaks of CyHV-3 in farmed carp in Japan at an individual fish level using experimental infections to inform parameter estimates. However, this model was highly theoretical and did not attempt to introduce realistic demography.

The aim of this study is to develop a biologically plausible transmission model of CyHV-3 to predict how it might impact on populations of common carp in south-eastern Australia if it were to be released as a biocontrol agent. For this we integrate detailed water temperature modelling (SECTION 1) with a reconstruction of carp demography at a sub-population level in each of catchments (SECTION 3). Furthermore, we assess the potential field effectiveness of the virus for biocontrol not only to achieve an initial knockdown of populations, but also for its capability to sustainably reduce them below the ecological damage thresholds which were defined through our habitat suitability modelling (SECTION 2).

Methods

The epidemiological model is an extension of the demographic model developed and described in SECTION 3 for common carp in Australia's waterways. As such it inherits the discrete, weekly time-step of the demographic model, where ageing, recruitment, movement and mortality are applied to the individual demographic stages and sub-populations of carp (see Table 4.1) that make up a whole-catchment population. The epidemiological component of the model is a set of continuous differential equations that describe the rates at which carp move through the disease states associated with CyHV-3. These equations are applied for a week at a time with new initial conditions set at the start of each week as calculated by the demographic model (see Figure 4.1) that accounts for changes in numbers due to demographic processes and movement. The carp in each sub-population are assumed to be sufficiently well-mixed such that contacts between infectious and susceptible carp occur in proportion to their frequency in the sub-population. A summary of the model parameters and their values can be found in Table 4.2.

Model assumptions

The model makes several, broad assumptions about the transmission and progression of CyHV-3 in Australian wild carp populations.. The first of these is that transmission of CyHV-3 occurs through direct, physical contact and that water-borne transmission is negligible in wild carp populations. It is certainly true that carp can become infected with CyHV-3 through immersion in water containing high concentrations of virus as this is a common challenge model for experimental studies into the susceptibility of carp to CyHV-3 (Adamek et al., 2019; Ito et al., 2014; Piackova et al., 2013). However, we deemed it unlikely that for wild carp living in free-flowing rivers that water-borne transmission would be effective, and that transmission would occur through physical contact between susceptible and infectious carp. We further reasoned that the most efficient type of physical contact for transmission of CyHV-3 would occur during pre-spawning aggregations of carp and during spawning activity itself. This led to a focus on the seasonal spawning behaviour of carp and observations of aggregations (see CarpMap Aggregation Survey below). Aggregations of immature carp also occur (Koehn et al., 2016), especially below weirs and barriers, and immature age-classes were also deemed susceptible.

The second key assumption is that there is no pre-existing heritable resistance to CyHV-3 amongst Australian wild carp populations. Carp strains derived from the Amur River subpopulation in East Asia show a significantly higher resistance to CyHV-3 than European strains derived from *C. carpio* (Dixon et al., 2009; Odegard et al., 2010; Shapira et al., 2005; Tadmor-Levi et al., 2017) but the extent to which Australian carp share any ancestry with the Amur carp is presently unknown. The uncertainties around the presence of genetic resistance to CyHV-3 are partly considered here by presenting only short and medium-term predictions of virus impact (<10 years from release date).

CyHV-3 replication is restricted by temperature with *in vitro* optimal virus growth observed to occur between 15 and 25ºC (Boutier et al., 2015). The optimal temperature range was modified slightly to define a permissive temperature range to occur between 16 and 28ºC. A third key assumption of the model is that when water temperature falls outside the permissive range transmission ceases and exposed or infected carp rapidly recover and enter a chronically (persistently) infected state; these carp also do not suffer any mortality due to the virus.

Governing equations

For the epidemiological component of the integrated model we modelled infection of carp with CyHV-3 using five disease states: susceptible (S), exposed (E), infectious (I), chronically infected (L) and secondarily infectious (Z), with the last state representing second and subsequent infections that can follow from repeated reactivation of the virus in chronically infected carp. The progression of individual carp through these disease states is shown in Figure 4.2. Eggs and Larvae (weeks 0-3) were assumed to be immune to the virus leaving four life-history stages (YOY_1, YOY_2, sub-adults and adults – see SECTION 3) vulnerable to infection. There are hence 20 state variables (5 disease states × 4 age-classes) for each sub-population, representing the number of carp in that sub-population and disease state with subscript *i* referring to the *i*th age-class. The governing system of differential equations is:

$$\frac{dS_i}{dt} = -\sum_{j=1}^{4} \lambda_{ij}(t,T)S_i$$

$$\frac{dE_i}{dt} = \sum_{j=1}^{4} \lambda_{ij}(t,T)S_i - \eta(T)E_i$$

$$\frac{dI_i}{dt} = \eta(T)E_i - \gamma(T)I_i$$

$$\frac{dL_i}{dt} = \big(1 - f_1(T)\big)\gamma(T)I_i + \big(1 - f_2(T)\big)\gamma(T)Z_i - \sigma L_i$$

$$\frac{dZ_i}{dt} = \sigma L_i - \gamma(T)Z_i,$$

(eqn 1)

where the total number of fish in age-class *i* is,

$$N_i = S_i + E_i + I_i + L_i + Z_i.$$

The force of infection from age-class j to age-class i is denoted $\lambda_{ij}(t, T)$ indicating that it varies over time (t; contacts vary seasonally) and is dependent on water temperature (T). The functional form is

$$\lambda_{ij}(t, T) = \nu(T) X_{ij}(t) \left(\frac{N_j}{A(t)}\right)^{\frac{1}{q}} \frac{I_j + Z_j}{N_j},$$

(eqn 2)

where $\nu(T)$ is the probability of transmission given contact occurs between a susceptible fish and an infectious one (this is set to 0 when water temperature is outside the permissive range), the $X_{ij}(t)$ are elements of a 4×4 matrix of contact rates between carp in age-class j and carp belonging to age-class i that scale with the (transformed) density of age-class j ($N_j/A(t)$), q is a parameter that determines whether contact rates scale linearly with density ($q = 1$) or are a saturating function of density ($q > 1$) or are effectively independent of density ($q \gg 1$; this case is also referred to as frequency-dependent transmission), and finally,

$$\frac{I_j + Z_j}{N_j}$$

is the fraction of contacts that are with an infectious carp of age-class j. The area of habitat available to carp, $A(t)$, can vary dramatically over time and was calculated on a weekly basis for each catchment and each subpopulation (see SECTION 2).

The matrix of contact rates is given by,

$$\begin{bmatrix} \frac{X}{m^3} & \frac{X}{m^4} & 0 & 0 \\ \frac{X}{m^4} & \frac{X}{m^2} & \frac{X}{m^3} & 0 \\ 0 & \frac{X}{m^3} & \frac{X}{m} & \frac{X}{m^4} \\ 0 & 0 & \frac{X}{m^4} & X\, s(M) \end{bmatrix}$$

(eqn 3)

where X is a base contact rate, m determines how contact rates scale with densities for the immature age-classes and $s(M)$ captures the effect of seasonal aggregation of adult carp on adult-to-adult contact rates for month M, which was inferred from the CarpMap aggregation survey results (see below). In the interests of model transparency, the contact matrix was assumed to be symmetric and further, it was assumed that physical contacts of the type likely to result in transmission of CyHV-3 would only be significant (due to differences in size and habitat use) for consecutive age-classes, e.g. between adult and sub-adult carp or between young of year and sub-adult carp; contact rates between non-consecutive age-classes were set to 0. When $m = 1$ the contact matrix simplifies and there is no distinction between inter-age-class and intra-age-class contact rates though contacts between non-consecutive age-classes are still 0 and adult-to-adult contact rates still vary with time of year (month M). For large values of m CyHV-3 becomes an infection of adults only. Values for the base contact rate, X, were constrained by ensuring that peak seasonal values for a within-season adults only R_0 (the number of adult carp infected by a single infectious adult carp over the course of its first infection with CyHV-3) were realistic (in the range 1—20; see below).

We note here that for most epidemics and infectious disease systems the age-specific contact structure of the host population is unknown though it can sometimes be inferred from observed outbreak data once an infectious disease has spread. For the spread of CyHV-3 in Australia in wild carp populations the uncertainties around contact structure will likely not be resolved until post-release.

CarpMap Aggregation Survey

The CarpMap Aggregation Survey was initiated by the need to better understand when, where and why carp come together (aggregate) in the rivers and waterbodies of South-eastern Australia. Members of the public were asked if they had seen carp aggregating in waterways over the past five years and invited to provide details via an online site (https://carpmap.org.au/carp/content). Taking the raw data (n=523) (as entered on the website by 8th of January 2019) a strong seasonal pattern is evident with people commonly reporting having seen aggregations in October and November (spring) but rarely in other months throughout the year. We used these data (see Table 4.3) as a proxy for seasonal changes in the frequency that aggregations of carp occur and hence for relative seasonal changes in the physical contact rates of carp ($s(M)$).

Calculations of R_0

The basic reproduction number is denoted R_0 and defined as the number of infected arising from a single typical infectious case in an otherwise susceptible population. In the context of CyHV-3 the calculation of R_0 is complicated because there are four age-classes of carp and they differ markedly in size, behaviour and habitat use (Koehn et al., 2016). Hence, a full calculation of R_0 would require a next generation matrix (see Diekmann and Heesterbeck (2000)) and an averaging over the four age-classes. It is further complicated by the possibility of virus reactivation leading to multiple infectious periods that occur throughout the relatively long lifespan of carp. We do not attempt to calculate a full R_0 for a typical infectious individual.

An indicative peak R_0 value for the adult age-class may be calculated that: (i) only considers the first infectious period, (ii) neglects transmission to and from all other age-classes apart from adults, and (iii), assumes that transmission is occurring during peak aggregation frequency (October). This indicative (peak) R_0 is relatively simple and can be derived using epidemiological reasoning. It is the product of the number of days spent infectious (during an initial infection only; $1/\gamma$), the probability of transmission given physical contact, and the seasonal peak in number of physical contacts with other adult carp (per adult per day). For finite values of q (i.e. when contact rate depends on carp density) the contact rate is calculated using the catchment scale median density of adults (D_A). This gives the formula,

$$\frac{1}{\gamma} \times \nu \times X \times s(10) \times \left(\frac{D_A}{160}\right)^{1/q},$$

where D_A varies across the five catchments (see Figure 4.3), $s(10)$ is the multiplicative factor accounting for the seasonal increase in contact rate due to aggregation (see Table 4.3) and the normalising constant of 160 is the reported density of carp (adult carp per ha) at Blue Springs Lake at the time of an outbreak of CyHV-3 (Thresher et al., 2018) and used as a rough reference point of adult carp density. The indicative R_0 can be interpreted as the initial exponential growth in infected adult carp during a spring epidemic of CyHV-3. The calculation is most accurate when $m \gg 1$.

Model Scenarios

For all model scenarios presented here the date of virus release was set to the 17th of October 2005 (dashed vertical orange line in Figures 4.4—4.7) which coincides with rising water temperatures in spring (on this date there had been at least 3 consecutive weeks when water temperatures were >16°C for all catchments) permissive for replication of CyHV-3. We simulated release in the model by adding 100 infectious adults to each sub-population in a catchment and the impact of the virus was measured by considering the reduction in abundance at the catchment-scale relative to the abundance predicted by the demographic model in the absence of the virus (see SECTION 3).

We defined an `optimistic' baseline scenario as one that included reactivation of the virus with onward infection and where contacts amongst carp were a saturating function of density ($q = 5$) and in which the virus spreads through all age-classes of carp ($m = 2$). In this scenario the base contact rate (X) was set to $X = 2$ so that indicative peak R_0 (calculated using median catchment adult density) values were lowest at 2.51 for the Glenelg catchment and highest at 12.78 for the Lower Murray. Because these R_0 values were all above 1 then outbreaks amongst adult carp were expected to occur for all catchments. This reflects an assumption that wild carp populations in Australia are at sufficiently high densities to trigger outbreaks of CyHV-3. All other epidemiological parameters were set to the values given in Table 4.2.

The alternative scenarios to the baseline were chosen to represent qualitatively different assumptions and differed from the baseline on only one point. We therefore considered scenarios, for example, in which reactivation did not occur ($1/\sigma = 0$), where contact rates were assumed to be (linearly) density-dependent ($q = 1$), and in which CyHV-3 only effectively spread amongst adult carp ($m \gg 1$). In addition to these we also ran scenarios to consider lower mortality due to first infection with the virus ($f_1 = 0.6$), no mortality due to second and subsequent infections with the virus ($f_2 = 0$) and lower contact rates ($X = 1$ and $X = 0.25$). Results for a subset of these scenarios are shown as time series of abundance aggregated at the catchment level for all 5 catchments (Figures 4.4—4.7).

Assessing field effectiveness

To assess the field effectiveness of CyHV-3 for biocontrol, we presumed there exists damage thresholds of carp biomass density (kg/ha) below which the presence of carp is not necessarily ecologically detrimental (SECTION 2). Recent research however has established that there is not a single threshold value, but this varies between ecosystems and on the ecosystem component being assessed, *viz*. vertebrates, invertebrates, aquatic vegetation and water quality (Vilizzi et al., 2015). For the purpose of the modelling we applied the same thresholds as for the habitat suitability modelling, i.e. 50 kg/ha for vertebrates and invertebrates, 100 kg/ha for aquatic vegetation and 150 kg/ha for water quality.

For each catchment we used the weekly mean abundance estimates for each subpopulation arising from the demographic modelling (SECTION 3) and converted these to an weekly mean biomass (i.e. kg) estimated by multiplying the total number of fish in each age class by the following mean weights: YOY1: 0.022 kg, YOY2: 0.022 kg, subadults: 0.523 kg and adults 2.618 kg. These mean weights were derived from the same survey data as used within SECTION 2 for estimating average weights for the two age classes (Larvae/YOY and Sub-Adult/Adult). The average weight of age class "0+" was allocated to Larvae/YOY stages, age class "1+" average weight was allocated to sub-adults and average weight of age class "Adult" were assigned to adults. We then divided this biomass for each subpopulation by the estimated mean area of the rivers and waterways (SECTION 1) for the subpopulation for that week, to arrive at a median density (kg ha^{-1}) for each subpopulation. We then performed the same calculation on the estimated population following a hypothetical release of the virus under the "baseline" scenario and used boxplots to compare the median for all the weeks of a given year for no-virus release biomass density and virus release biomass density.

Four release scenarios were then undertaken and analysed, corresponding to different periods of the southeast Australian drought cycle: during a wet period, (spring 1995), the beginning of Millennial drought (spring 2000), the mid Millennial drought (spring 2005) and end of the Millennial drought (spring 2010). As we consider that the most plausible epidemiological model is "Baseline", we only applied the conversions to this model. However, estimates were calculated for 17 scenarios for the 5 catchments. The scenarios varied for each catchment depending on the availability of time-series demography data. The number of subpopulations which were below the three thresholds 50 kg ha^{-1}, 100 kg ha^{-1} and 150 kg ha^{-1} for each subpopulation and for each year both with and without the virus were then calculated, and number of weeks that the virus reduced the population below the three damage thresholds were estimated.

Results

The results of the demographic model without any virus release are presented and discussed in SECTION 3 and are used here to evaluate the impact of virus release on carp abundance (grey shaded curves in the background of Figures 4.4—4.7). For the calculations of an indicative peak R_0 for CyHV-3 we used median adult carp densities: box and whisker plots for each catchment (showing the median, interquartile range and outliers) are shown in Figure 4.3. As noted in SECTION 3 there are significant differences between the catchments with the Glenelg carp population being at the lowest density (though also growing), the Lachlan catchment carp population undergoing dramatic changes in density (in response to the severe flood-drought cycle experienced there over the last 2-3 decades) and the sub-catchments of the Murray river being the most stable and having the highest carp densities.

We present results for the baseline scenario (Figure 4.4) and alternative scenarios with no reactivation (Figure 4.5), higher survival of infected carp (Figure 4.6) and linear density-dependent contact rates (Figure 4.7). In the baseline scenario, the virus consistently suppresses carp abundances to between 40 and 80% of that expected in the absence of the virus. This occurs for all 5 catchments and is not conditional on the year of release (results not shown). A spring release of infectious carp always causes an immediate epidemic to occur in all age-classes causing abundance to fall by ~70% with almost all carp in the susceptible stage classes (young-of-year and older) being exposed to CyHV-3. Surviving carp are chronically infected and cannot be reinfected and the epidemic dies out after 6-8 weeks as the number of susceptible carp declines. The carp population then recovers somewhat over the summer and autumn through continued recruitment and higher survival rates of immature fish (due to density-dependent release). While some transmission occurs amongst the immature fish in autumn (while temperatures are still permissive) the virus truly goes extinct over winter (the numbers of infectious and exposed carp are 0 in all age-classes). The initial epidemic is followed by annual spring and autumn outbreaks amongst immature carp. Adult carp do also become infected during these outbreaks but the numbers of infected adults are much smaller – at least one order of magnitude smaller – than in the initial outbreak with very few adult carp still susceptible to infection. Amongst immature carp the subsequent outbreaks tend to be smaller than the initial outbreak too, but this varies between catchments and years. In the Lachlan catchment, for example, larger outbreaks occur later in the timeseries coinciding with the end of the millennial drought and surges in recruitment of susceptible carp.

In the case of the alternative scenario without reactivation of the virus and onward infection (Figure 4.5) there is the same initial epidemic but the impact on carp abundance is short-lived and there are no subsequent outbreaks. Within five years the virus no longer significantly suppresses the carp population. SECTION 3 present more detailed results relevant to this scenario since it is equivalent to a single mortality event.

Model outcomes are also shown for when the virus causes lower mortality (60% of infected fish die rather than 80%) (Figure 4.6) and when contact rates between carp scale linearly with density (Figure 4.7). These results illustrate sensitivity to the virus mortality rate and model assumptions about the nature and frequency of physical contacts between carp. In both cases virus impact is reduced, and the suppression levels are at most 50%. When contact rates scale linearly with density then this has a protective effect for the Glenelg catchment, for example, where densities are lowest (Figure 4.3) and suppression levels are in the range of just 20-30%. Similarly, reducing the base contact rate plays out most clearly at the subpopulation level (results not shown) where the virus spreads in some (high density) subpopulations and not in others. The impact at the catchment level is then a matter of what proportion of subpopulations have high enough densities to support outbreaks. Interestingly this can mean that CyHV-3 is predicted to spread more effectively during periods of drought which can concentrate carp and increase density while there is a declining number of carp.

With respect to the field effectiveness of CyHV-3 as a biocontrol agent to reduce populations of carp below the variously estimated damage functions, our modelling shows that this varied considerably between catchments (Figure 4.8). In the Lachlan catchment where 65% of the subpopulation-weeks were above the intermediate 100 kg/ha damage threshold, a hypothetical release of the virus reduced this to 12% (Table 4.6). A comparable result was shown for the Moonie catchment (42% above the intermediate threshold without virus release and 10% with virus release). In the Murray River, with much higher biomass density, a virus release was not as successful in reducing densities below the intermediate threshold (Mid Murray: 91% reduced to 47% and Lower Murray: 99% to 43%). In the Glenelg, the biomass density was only above the 100 kg/ha threshold in 12% of the subpopulation-weeks, with the virus reducing this to 5%, but note that this catchment had different demography as carp only entered the lower part of the river around 2000, and thus the population was still increasing over the simulation period (Figure 4.8). Comparable results were found for each catchment for the other release scenarios of the drought cycle (Supplementary Tables S1-S3).

Discussion

To our knowledge this is the first attempt to use an integrated habitat suitability-epidemiological-demographic model to predict the potential outcome of a biocontrol agent for a vertebrate pest; and it is particularly ambitious because it uses a landscape ecology approach such that the spatial heterogeneity of real landscapes is incorporated. The integrated model has been successfully applied to 5 very different catchments and we emphasise that the same model has been applied with no manual adjustments to any of the parameters. This has given us confidence that the demographic model (SECTION 3) has been effective in capturing the key demographic processes that govern the abundance of wild carp populations across Australia, and subsequently that the integrated model can give us insight into the likely consequences of releasing CyHV-3, keeping in mind model uncertainty and parameter uncertainty.

The purpose of this modelling study is to provide insight into the likely impact of CyHV-3 and how this might qualitatively depend on model assumptions that attempt to capture the relevant biology of the virus and its host population. As such it investigates model uncertainty rather than parameter uncertainty and we have not attempted to perform a formal sensitivity analysis such as calculations of Sobol's indices (Johnstone-Robertson et al., 2017). Such an exercise minimally requires that (i) ranges are chosen for all parameters, and (ii) model output is reduced to a handful of well-defined quantitative outcomes. In the absence of field data on outbreaks of CyHV-3 amongst wild carp, or experimental data from transmission studies, we could not reasonably define ranges for all parameters in the model. Secondly, the model outputs for the Mid Murray sub-catchment, for example, are a set of $27 \times 6 \times 4 = 648$ timeseries (number of sub-populations times number of disease states times number of susceptible age-classes) which we have reduced here by pooling results at the catchment scale. It is therefore challenging to define a reasonably small set of model outputs on which to perform a sensitivity analysis. In this study we have visualised model outcomes as timeseries rather than summary model outputs to better understand where qualitative differences occur in virus dynamics.

The strongest conclusion of the modelling is that the medium-term impact of CyHV-3 in terms of carp abundance is highly sensitive to whether reactivation occurs and allows the virus to persist beyond the first year of release. Such persistence causes ongoing seasonal epidemics and mortality, mostly amongst immature age-classes of carp that were not previously exposed to the virus. These results are not sensitive to the rate at which recrudescence occurs, just that it does occur. Intuitively, reactivation is equivalent to the introduction of small numbers of infected fish that spark off further outbreaks when there is enough build-up of susceptible fish through recruitment and when water temperatures are permissive. This can be seen happening in Figures 4.3, 4.5 and 4.6 that show strong seasonality in infection with significant numbers of infected appearing in the spring of each year (again, more evident in the immature age classes). With reactivation and onward infection, the model predicts that the virus will cause continued suppression of the carp population until either virus or host evolve to reduce mortality rates or (equivalently) if heritable resistance develops in the carp population.

The predicted virus impact at the catchment level varies between catchments and across different years of release corresponding to periods of drought and recovery; the broad picture is that the less productive periods and sites represent carp populations that are less resilient to virus mortality (and so the impact is greatest with 60-80% suppression) while the more productive periods and waterways are more resilient (and the impact is more like 40-60%). It is important too to realise that the time series of abundance (Figures 4.3—4.6) represent the summed populations of carp that show the outcome of virus release at the catchment level, yet this outcome may not be representative (or only rarely representative) of the outcome for any of the subpopulations within the catchment. This is because infectious diseases tend to display threshold behaviour whereby either very little happens or an epidemic `takes off'. Hence, in any catchment the impact on sub-populations could be more severe, or much less severe, than that predicted by the catchment-level results.

Another important observation is that despite the virus continuing to suppress the population, all scenarios with virus persistence suggest that noticeable fish die-offs will only occur during the first epidemic. Subsequent seasonal epidemics do occur in all age classes but in the adult population they are at least one order of magnitude smaller. This is consistent with the observations in the Northern hemisphere detailed by Thresher et al. (2018) that ongoing die-offs were not observed. However, the modelling reveals that this is not a sign that the virus has stopped suppressing carp populations, and instead the opposite is occurring.

The predicted impact of the virus on carp populations is demonstrably sensitive to the mortality rates due to first infection with the virus (f_1) and the two transmission parameters – the base contact rate of adult carp per day (X) and the exponent q which determines how transmission rates scale with densities. The sensitivity to the latter two parameters is expected because together they determine how contagious CyHV-3 is. We note that the baseline scenario predicts a timing (spring) and duration (4-6 weeks) of predicted epidemics that is consistent with the epidemics in wild populations observed in North America (Thresher et al., 2018) and Japan (Hara et al., 2006).

Although our modelling results are consistent with overseas results, it is important to note several limitations. The first, which applies to all mathematical models of infectious diseases is the uncertainty around the key epidemiological rates whereby infected fish pass from the susceptible to the exposed to infectious and to the latent and recrudescent classes (Figure 4.2). Ideally these parameters, and particularly the reproductive number (R_0) are estimated from analysis of surveillance outbreak data recording the timing in which individuals develop symptoms (White and Pagano, 2008). However, data of this type is extremely difficult to obtain from outbreaks of disease in wildlife, and to date the only data available for CyHV-3 in wild carp are limited records of daily recordings of mortality (Hara et al., 2006). Laboratory-based infection trials are potentially more informative, but to date most have reported only the proportion of fish dying each day post infection (Sunarto et al., 2011; Yuasa et al., 2008). Furthermore, experimental infection trials studies generally use small juvenile fish for which it is questionable to what extent inferred parameter values can be extrapolated to adult fish, particularly given the agreed importance of reproductive aggregations in facilitating transmission. Nevertheless, the basic epidemiology of the disease is known, and although there remains a number of uncertainties, we have reasonable confidence that our model can provide fit-for-purpose predictions to enable the development of a release strategy. We do however advise that the output of modelling should be, at this stage, used cautiously for detailed operational planning and ideally, if a decision is made to release the virus, then its parameters be re-estimated through detailed field data collection of outbreaks post-release.

An underlying assumption of the epidemiological modelling is that all fundamental aspects of the host-pathogen interaction of CyHV-3 in wild common carp in Australia will be essentially the same as has been observed in overseas countries. This applies particularly to the Japanese experience, where researchers developed a coherent conceptual model linking spring aggregations with latently infected survivors which thus enabled seasonal transmission and persistence (Uchii et al., 2014; Uchii et al., 2011). These concepts are central to our mathematical model and its key prediction that the virus will persist in the population and continue to suppress populations as a result of ongoing mortalities in naïve juveniles as they enter the population and are exposed to persistently infected adults. If however, there was some unique feature of the host-pathogen interaction of common carp in Australia which prevented latency in recovered fish – i.e. they become truly immune to further infection – this could lead to herd immunity effects preventing onward infections. Combined with the reproductive potential of the surviving adult carp, the result would be a full recovery of populations within a few years (Becker et al., 2019). Our modelling fully agrees with this possibility (Figure 4.5), but it is difficult to see how this would occur, given that Australian carp are genetically so related to European cultured carp in which latency has been demonstrated (Baumer et al., 2013) and an infection trial of Australian carp using the Indonesian strain of CyHV-3 – which is the one that will be used if a decision to release goes ahead – showed persistence indicative of latency (Sunarto et al., 2014).

The field effectiveness analysis predicts considerable diversity of outcomes between catchments, which in the Lachlan results in a reduction of carp biomass to below the 100 kg/ha threshold irrespective of under which drought cycle scenario the virus is released. In the Glenelg and in most of the Moonie, the median biomass density has never reached this damage threshold and it is questionable whether the virus needs to be released in a managed manner. In the Lower Murray, where exceptionally high biomass density of carp occur in some sub-populations, the modelling indicates that the virus by itself may not reduce the populations below the damage threshold. In this instance there is a good argument for first reducing the population by commercial harvest before releasing the virus, which would also limit the possibility of adverse water quality impacts such as anoxia and cyanobacterial blooms. These examples indicate considerable potential for tailoring the release of the virus to the particularities of each catchment, i.e. adaptive management, an approach which has been advocated for other activities designed to deliver ecological restoration to the MDB (King et al., 2010).

A beneficial consequence of natural transmission occurring principally in the spring is that it will enable more precise operational planning for release into catchments at defined times. However, this also presents a challenge in that the window for release may only be 2-3 months, and as the data from the CARPMAP is currently insufficient to build a predictive model of where aggregation events might occur, then there will need to be rapid response to aggregation sightings to achieve efficient virus transmission within these. In practice, developing cost-effective release will also require adaptive management, probably combining elements of predictive water temperature modelling (SECTION 1) and a carp aggregation alert system using a website similar to CARPMAP. However, an alternative option that is worth exploring is the inoculation of adult wild carp with the virus in winter when the non-permissive water temperature would not allow it to induce disease, which would occur later as the water warms in the spring. Furthermore, although the inoculated fish would be carrying the virus in a dormant state, their behaviour would not be expected to change, and thus they would engage in normal mating and aggregation behaviour. This concept of a "Trojan carp" release will need further research to prove that it is operationally viable, but if found feasible, then the broad release strategy suggested by our modelling could then be fully operationalised.

Conclusion

In the context of the overall objective of our integrated ecological-epidemiological study to develop a strategy informing when, where and how to release CyHV-3, our modelling provides a rational basis for its development. Most easily answered is the "when" which is recommended to be in the spring, as although the temperatures of the rivers and waterbodies of south-eastern Australia are in the permissive range for CyHV-3 activity for much of the summer and autumn (SECTION 1), we predict based on our assumption of the importance of skin-to-skin contact for effective transmission, that a spring release will cause epidemics of the size leading to significant knockdowns. Regarding "where" to release the virus, the field effectiveness analysis suggests that priority for release should be given to areas where carp are above the damage threshold and the virus can be expected to bring it below this, either by itself, or with complementary measures such as commercial fishing. This leaves the main issue to resolve being the "how" as our modelling indicates the importance of effective deployment in the spring at the time where aggregation events are occurring to achieve the required knockdowns. Thus we recommend that experiments be undertaken to determine if the "Trojan carp" concept of winter inoculations of the virus might be an effective mechanism of delivery.

Acknowledgements

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We thank Peter West (NSW Department of Primary Industries), Jamie Allnutt (National Carp Control Plan) and Mike Newton (NewtonGreen Technologies) for the development of the CarpMap Aggregation Survey online survey application; and to Stephen Taylor (CSIRO-Data61) for improvements and curation of the *R* code developed to run the integrated demographic-epidemiological model. We also thank Dr Joy Becker (University of Sydney) for insightful discussions of the host-pathogen interaction of CyHV-3 and common carp.

Tables

Table 4.1

Key model terms and their definitions

Terminology	
Sub-population	Discrete populations within the metapopulation which are connected by movement of fish. All demographic and epidemiological processes are assumed to occur homogeneously within a sub-population and contacts between fish within a sub-population are assumed to be well-approximated by random mixing.
(Demographic) Stage	Life-history stages for carp. Delineated as Larvae (L), 2 Young-of-Year stages (YOY_1 & YOY_2), Sub-adults (SA), and adults (A). Each stage is characterised by different survival (density independent and density dependent) and movement rates, with adult reproducing and YOY1 and older being susceptible to the virus. See SECTION 3.
(Disease) State	Epidemiological states for carp. Delineated as susceptible (S), exposed (E), infectious (I), chronically infected (L) and secondarily infectious (Z) following reactivation of the virus. Note that eggs and larvae (weeks 0-3) are immune to the virus.

Table 4.2

Epidemiological parameters

Parameter description	Parameter symbol	Value	Notes/References
Force of infection from age-class j to age-class i	$\lambda_{ij}(t,T)$	A function of time, t, and water temperature, T	Not a parameter but included here for clarity, see eqn 2.
Base contact rate (number of physical contacts per day with other adult carp when adult density is 160 per ha)	X	0.25, (1) or 2 contacts per day	Values chosen for convenience and that generate plausible values for the indicative R_0 – see main text.
Scaling parameter for age-dependent contact rates	m	2 (or 10)	Arbitrarily chosen – there is no information on age-dependent contact rates for common carp.
Probability of transmission given physical contact	ν	0.5 (when water temperatures are permissive)	There is no information on this parameter; value chosen as the midpoint between 0 and 1.
Scaling parameter determining the effect of host densities on contact rates	q	5 or 1	See main text. A value of 1 corresponds to the common assumption of density-dependent transmission. A value of 5 (>1) corresponds to the transmission rate saturating with host density.
Incubation period	$\frac{1}{\eta}$	1.5 days (when water temperatures are permissive)	Omori & Adams (2011); unpublished data (CSIRO AAHL).
Infectious period	$\frac{1}{\gamma}$	5 days (when water temperatures are permissive)	Omori & Adams (2011).
Mortality rate following a first infection	f_1	0.8 or 0.6 (when water temperatures are permissive)	McColl et al (2017).
Mortality rate following a subsequent infection	f_2	0.05 (when water temperatures are permissive)	Arbitrarily chosen. There is no information on this parameter but mortality following reactivation and a secondary infection is assumed to be rare.
Period carp remain chronically infected before they experience recrudescence	$\frac{1}{\sigma}$	1000 days	Arbitrarily chosen. There is no information on this parameter, but reactivation was assumed to be rare.

Table 4.3

Seasonal changes in carp aggregation frequency

Month	$s(t)$
January	0.948
February	0.720
March	0.588
April	0.288
May	0.204
June	0.180
July	0.228
August	0.132
September	0.924
October	3.456
November	2.880
December	1.464

Table 4.4

Median adult carp densities (per ha)

Catchment	Density
Glenelg	3.38
Lachlan	40.1
Lower Murray	87.6
Mid Murray	77.9
Moonie	28.1

Table 4.5

The model defining parameters (in bold) for the scenarios shown in Figures 4.4 – Figure 4.7. Included are three scenarios which were run, but the results are not shown.

Parameter	**Baseline / optimistic (Fig 4.4)**	**No reactivation or recrudescence (Fig 4.5)**	**Lower initial mortality) (Fig 4.6)**	**Density dependent contact rates (Fig 4.7)**	**CyHV-3 only spreads amongst adults (results not shown)**	**No mortality following virus reactivation (results not shown)**	**Low contact rate / low transmission) (results not shown)**
Base contact rate (X)	2	2	2	2	2	2	**1 or 0.25**
Scaling parameter for age-dependent contact (m)	2	2	2	2	**10**	2	2
Transmission probability (v)	0.5	0.5	0.5	0.5	0.5	0.5	0.5
Scaling parameter for density dependent contact rates (q)	5	5	5	**1**	5	5	5
Initial mortality (f_1)	0.8	0.8	**0.6**	0.8	0.8	0.8	0.8
Mortality following virus reactivation (f_2)	0.05	0.05	0.05	0.05	0.05	**0**	0.05
Rate of recrudescence (σ)	0.001	**0**	0.001	0.001	0.001	0.001	0.001

Table 4.6

Data as for Figure 4.8 showing overall field effectiveness for a hypothetical release of the virus in the spring of 2005, during the middle of the Millennial drought. (a). Scenario attributes, showing the calculation for the number of scenario subpopulation-weeks; (b) The number of subpopulation-weeks where the biomass density is above each of the three damage thresholds, with the percentage in parenthesis being this number divided by the total number of subpopulation-weeks.

a. Scenario attributes

	Moonie River	Lachlan River	Mid Murray River	Lower Murray River	Glenelg River
Date of virus release	17/10/2005	17/10/2005	17/10/2005	17/10/2005	31/10/2005
Number subpopulations	15	50	27	29	29
Number of weeks in the scenario	503	521	521	521	521
Scenario sub-populations x weeks	7,545	26,050	14,067	15,109	5,210

b. Number of weeks each sub-population are above the three damage thresholds (plus percentages)

		Moonie River	Lachlan River	Mid Murray River	Lower Murray River	Glenelg River
Lower damage threshold (50 kg ha^{-1})	**Without virus**	5,701 (75.56%)	24,103 (92.53%)	13,391 (95.19%)	15,094 (99.90%)	1,626 (31.21%)
	With virus release	2,210 (29.29%)	7,493 (28.76%)	10,598 (75.34%)	14,754 (97.65%)	439 (8.43%)
Intermediate damage threshold (100 kg ha^{-1})	**Without virus**	3,168 (41.99%)	16,820 (64.57%)	12,747 (90.62%)	15,020 (99.41%)	640 (12.28%)
	With virus release	723 (9.58%)	3,041 (11.67%)	6,549 (46.56%)	11,068 (73.25%)	282 (5.41%)
Upper damage threshold (150 kg ha^{-1})	**Without virus**	1,969 (26.10%)	8,733 (33.52%)	11,108 (78.96%)	14,753 (97.64%)	403 (7.74%)
	With virus release	301 (3.99%)	1,741 (6.68%)	4,168 (29.63%)	6,498 (43.01%)	162 (3.11%)

Figures

Figure 4.1

Conceptual diagram of the combined epidemiological and demographic models and data analysis. Dashed boxes indicate separate models/code

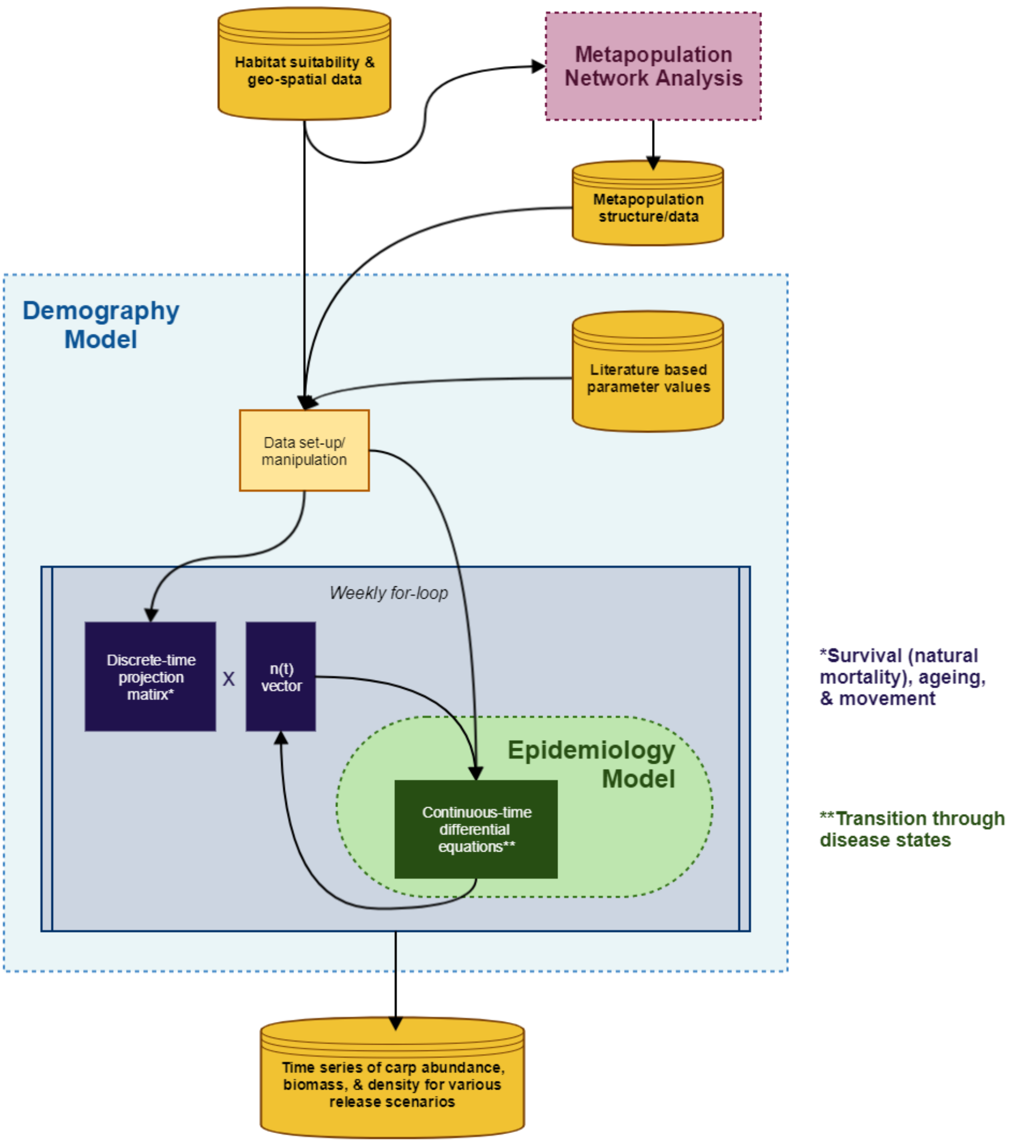


Figure 4.2

Conceptual diagram of the disease states and the progression of individual carp through them. The disease states are susceptible (S), exposed (E), infectious (I), chronically (persistently) infected (L) and secondarily infectious (Z), the latter indicating an infectious state following reactivation of the virus.

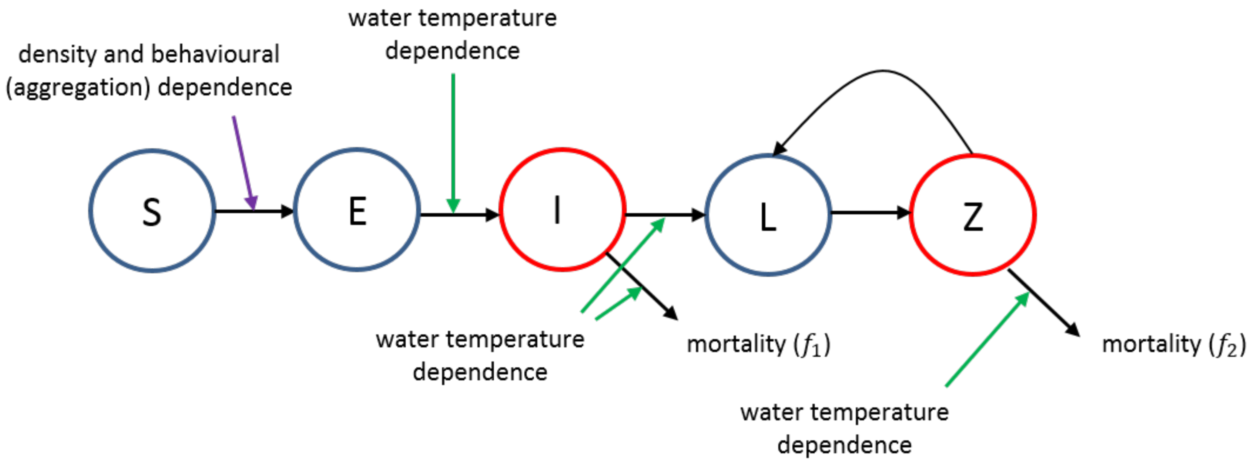


Figure 4.3

Box and whisker plots for adult carp densities at the subpopulation scale averaged over a season (period from June of one year to July of the next) and including all subpopulations having an area of available habitat greater than 2 hectare. Whiskers are displayed for the 5th and 95th percentiles. Within the Lachlan 8 outliers were not displayed due to y-axis constraints.

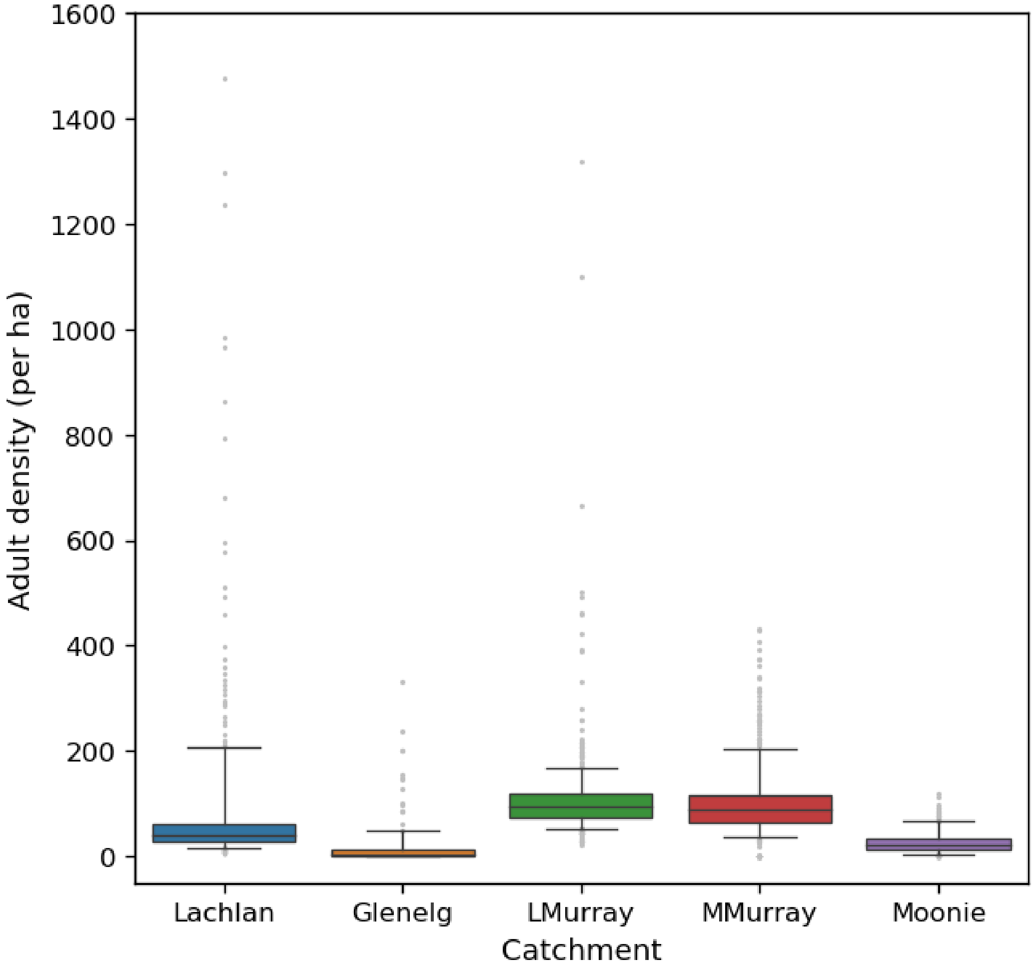


Figure 4.4

Baseline scenario epidemiological model output (see Table 4.5 for parameter values) for the 5 catchments following a virus release on the 17^{th} of October 2005 (dashed vertical orange line; release date coincides with rising water temperatures in spring and 100 infectious adults are released in each sub-population) given as time series of adult and sub-adult abundance (left-hand column) and time-series of numbers of infectious, exposed, chronically infected and secondarily infectious carp divided into mature (Mat.) and immature (Imm.) age-classes (right-hand column). Catchment labels refer to the Moonie River catchment (M), the Lachlan River catchment (L), a mid and lower section of the Murray River (respectively MM and LM), and the Glenelg River catchment (G).

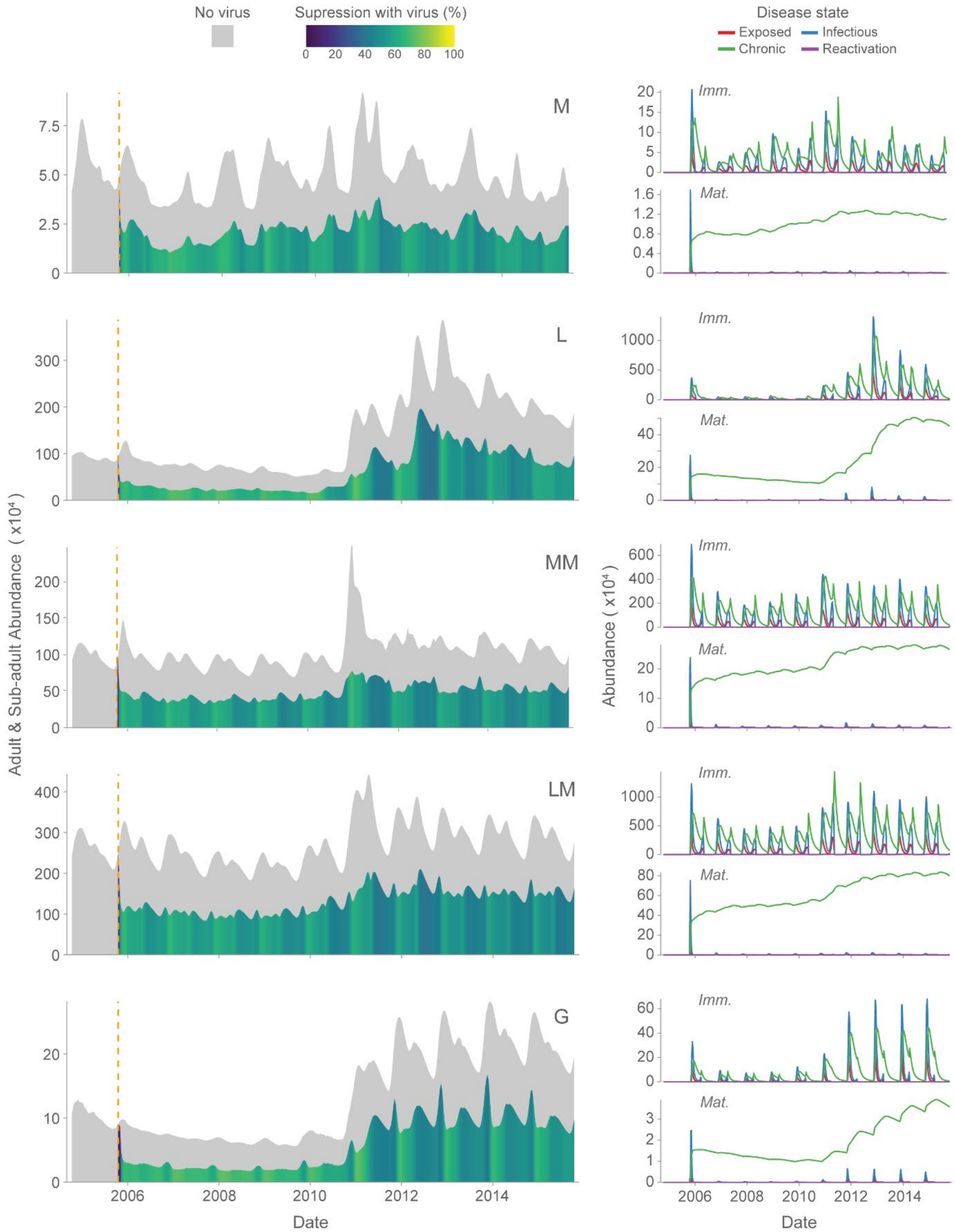

No virus
Supression with virus (%)
0 20 40 60 80 100
Disease state
Exposed
Infectious
Chronic
Reactivation
M
L
MM
LM
G
Imm.
Mat.
Adult & Sub-adult Abundance (x10⁴)
Abundance (x10⁴)
2006 2008 2010 2012 2014
Date

Figure 4.5

Scenario as for the baseline (Figure 4.4), but without reactivation of persistently infected survivors (i.e. 1/sigma = 0).

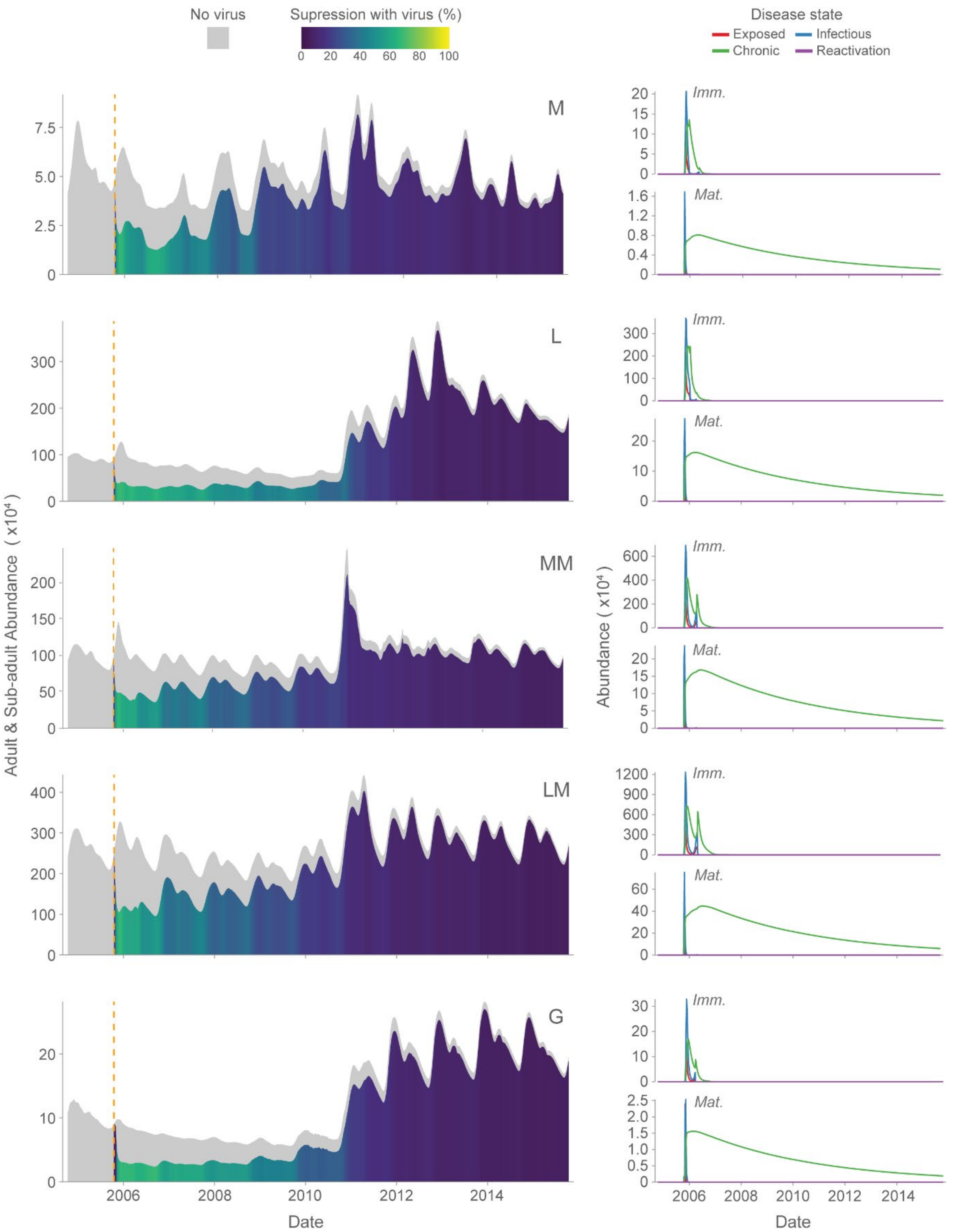


Figure 4.6

Scenario as for the baseline (Figure 4.4), but with a lower initial mortality in previously susceptible carp (i.e. f1 = 0.6).

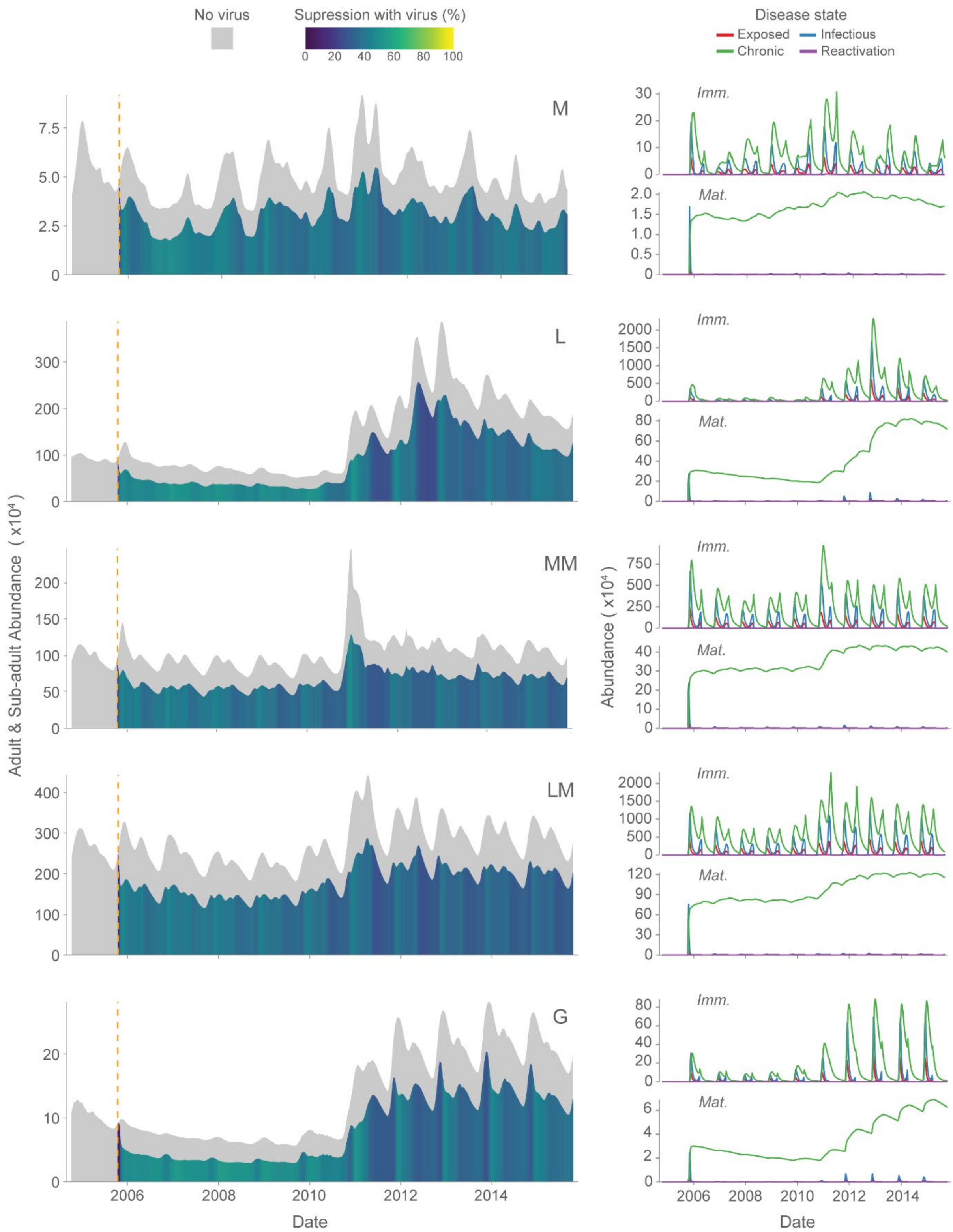


Figure 4.7

Scenario as for the baseline (Figure 4.4), but with density-dependent contact rates (i.e. q = 1).

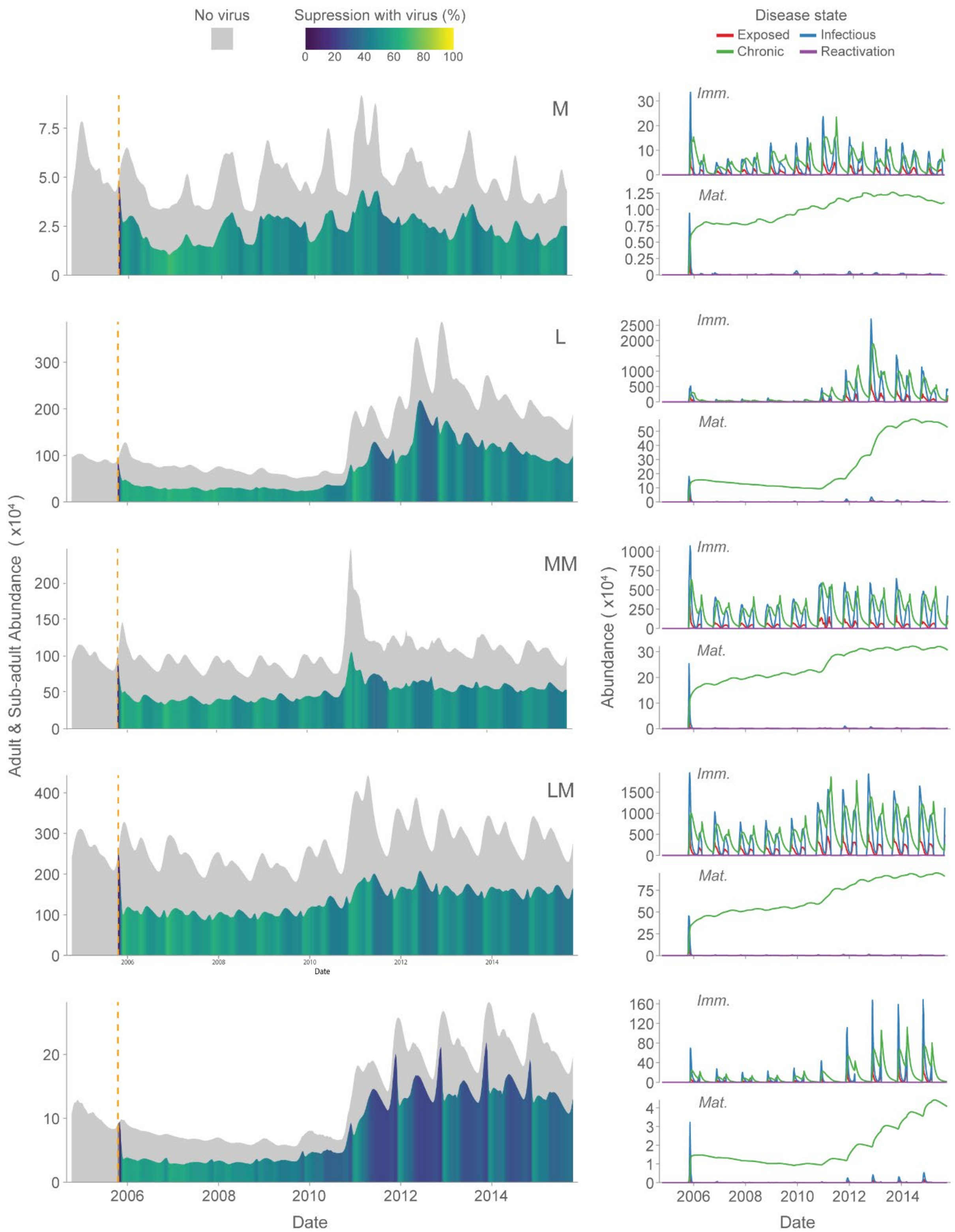
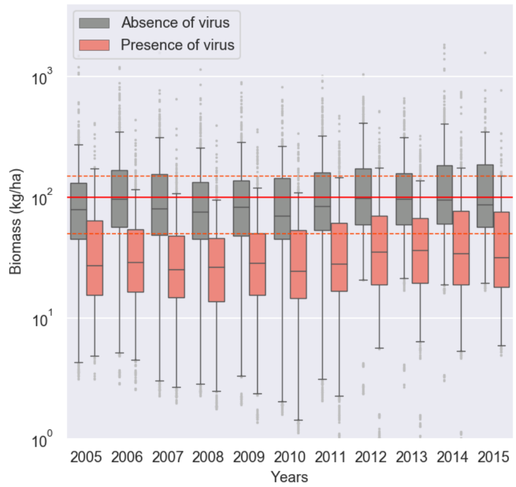


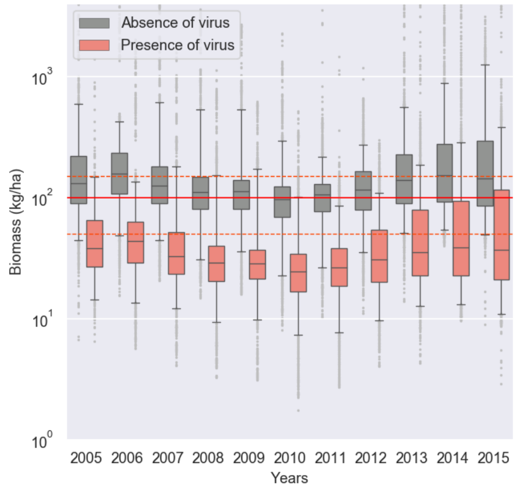
Figure 4.8

Field effectiveness of the CyHV-3 in reducing the modelled biomass density of carp to below the three presumed damage thresholds (50 kg/ha: lower dashed line, 100 kg ha: solid red line and 150 kg/ha: upper dashed line) in the study catchments. Shown is the scenario corresponding to the release of the virus in the Mid Millennial Drought (Spring 2005). Non-release populations are derived from the demographic reconstruction described in SECTION 3. Data for the figures is given in Table 4.6.

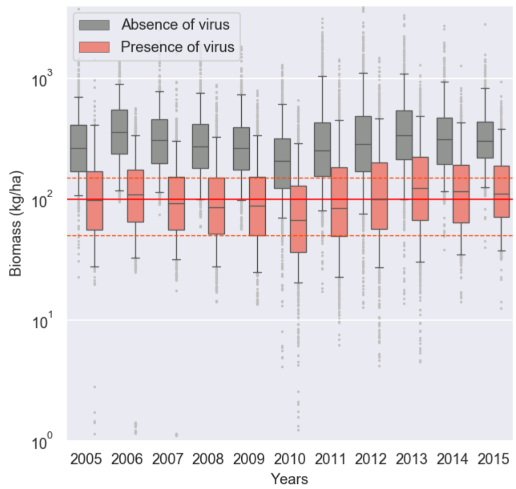
a. Moonie River catchment



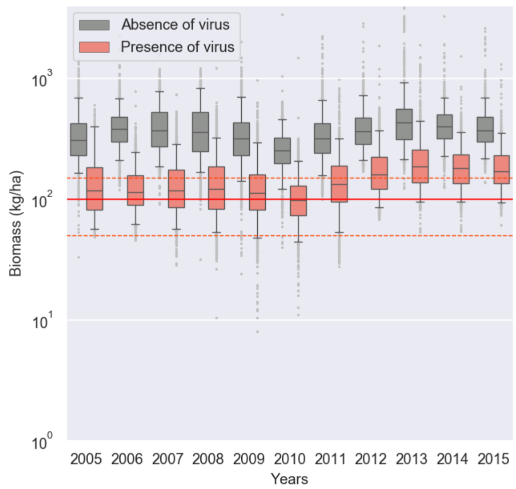
b. Lachlan River catchment



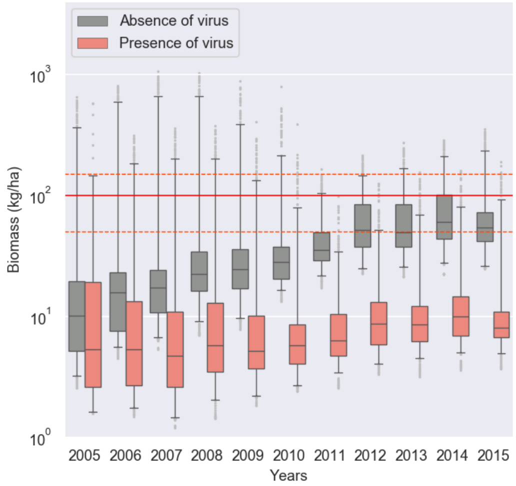
c. Mid Murray River



d. Lower Murray River



e. Glenelg River



Supplementary tables

Table S1 – Field effectiveness Spring 1995 release

Summary data, comparable to Table 4.6, for the field effectiveness of a spring release of the virus during a Wet period of the south-eastern Australian drought cycle. Note that the Lachlan and Glenelg River catchments were not modelled due to absence of hydrological data (the Lachlan) and uncertainty over the status of the fish population (the Glenelg).

a. Scenario attributes

	Moonie River	Lachlan River	Mid Murray River	Lower Murray River	Glenelg River
Date of virus release	9/10/1995	n/a	9/10/1995	9/10/1995	n/a
Number subpopulations	15	n/a	27	29	n/a
Number of weeks in the scenario	521	n/a	521	521	n/a
Scenario sub-populations x weeks	7,815	n/a	14,067	15,109	n/a

b. Number of times sub-populations are above each of the damage thresholds (plus percentages)

		Moonie River	Lachlan River	Mid Murray River	Lower Murray River	Glenelg River
Lower damage threshold (50 kg ha^{-1})	**Without virus**	4,968 (63.57%)	n/a	13,421 (95.41%)	15,101 (99.95%)	n/a
	With virus release	1,391 (17.80%)	n/a	11,905 (84.53%)	14,844 (98.25%)	n/a
Intermediate damage threshold (100 kg ha^{-1})	**Without virus**	2,467 (31.57%)	n/a	13,249 (94.18%)	15,004 (99.31%)	n/a
	With virus release	372 (4.76%)	n/a	7,593 (53.98%)	11,842 (78.38%)	n/a
Upper damage threshold (150 kg ha^{-1})	**Without virus**	1,223 (15.65%)	n/a	12,436 (88.41%)	14,715 (97.39%)	n/a
	With virus release	129 (1.65%)	n/a	4,715 (33.52%)	7,016 (46.44%)	n/a

Table S2 – Field effectiveness Spring 2000 release

Summary data, comparable to Table 4.6, for the field effectiveness of a spring release of the virus at the beginning of the Millennial drought in south-eastern Australia. Note that the Glenelg River catchments was not modelled due to uncertainty over the status of the carp population in that year.

a. Scenario attributes

	Moonie River	Lachlan River	Mid Murray River	Lower Murray River	Glenelg River
Date of virus release	9/10/2000	9/10/2000	9/10/2000	9/10/2000	n/a
Number subpopulations	15	50	27	29	n/a
Number of weeks in the scenario	521	521	521	521	n/a
Scenario sub-populations x weeks	7,815	26,050	14,067	15,109	n/a

b. Number of times sub-populations are above each of the damage thresholds (plus percentages)

		Moonie River	Lachlan River	Mid Murray River	Lower Murray River	Glenelg River
Lower damage threshold (50 kg ha^{-1})	**Without virus**	5,512 (70.53%)	24,460 (93.93%)	13,445 (95.58%)	15,092 (99.89%)	n/a
	With virus release	1,932 (24.72%)	8,665 (33.26%)	11,600 (82.46%)	14,804 (97.98%)	n/a
Intermediate damage threshold (100 kg ha^{-1})	**Without virus**	2,839 (36.33%)	18,577 (71.31%)	13,024 (92.59%)	14,994 (99.24%)	n/a
	With virus release	597 (7.64%)	3,447 (13.23%)	7,354 (52.28%)	10,917 (72.25%)	n/a
Upper damage threshold (150 kg ha^{-1})	**Without virus**	1,608 (20.58%)	10,704 (41.09%)	11,755 (83.56%)	14,643 (96.92%)	n/a
	With virus release	208 (2.66%)	1,898 (7.29%)	4,629 (32.91%)	6,218 (41.15%)	n/a

Table S3 – Field effectiveness Spring 2010 release

Summary data, comparable to Table 4.6, for the field effectiveness of a spring release of the virus at the end of the Millennial drought in south-eastern Australia.

a. Scenario attributes

	Moonie River	Lachlan River	Mid Murray River	Lower Murray River	Glenelg River
Date of virus release	11/10/2010	11/10/2010	11/10/2010	11/10/2010	8/11/2010
Number subpopulations	15	50	27	29	29
Number of weeks in the scenario	244	321	346	373	376
Scenario sub-populations x weeks	3,660	16,050	9,342	10,817	3,760

b. Number of times sub-populations are above each of the damage thresholds (plus percentages)

		Moonie River	Lachlan River	Mid Murray River	Lower Murray River	Glenelg River
Lower damage threshold (50 kg ha^{-1})	**Without virus**	2,851 (77.90%)	14,976 (93.31%)	8,849 (94.72%)	10,813 (99.96%)	1,946 (51.76%)
	With virus release	1,097 (29.97%)	5,754 (35.85%)	7,051 (75.48%)	10,637 (98.34%)	308 (8.19%)
Intermediate damage threshold (100 kg ha^{-1})	**Without virus**	1,626 (44.43%)	10,568 (65.84%)	8,481 (90.78%)	10,784 (99.69%)	576 (15.32%)
	With virus release	388 (10.60%)	2,726 (16.98%)	4,514 (48.32%)	8,751 (80.90%)	110 (2.93%)
Upper damage threshold (150 kg ha^{-1})	**Without virus**	1,026 (28.03%)	6,253 (38.96%)	7,386 (79.06%)	10,657 (98.52%)	245 (6.52%)
	With virus release	160 (4.37%)	1,601 (9.98%)	2,916 (31.21%)	5,651 (52.24%)	25 (0.66%)

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