LA TROBE UNIVERSITY **Centre for Freshwater Ecosystems** **NIWA** Taihoro Nukurangi

MMCP Collaboration Final Report 2019 -
Impact of hydrology and climate on the growth dynamics of Murray cod and Golden perch

Prepared by: Rick Stoffels, Kyle Weatherman, Jason Thiem, Gavin Butler, John Morrongiello, Nick Bond, Wayne Koster, R. Keller Kopf, Nicole McCasker, Qifeng Ye, Brenton Zampatti and Ben Broadhurst

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The Centre for Freshwater Ecosystems
La Trobe University Campus
Wodonga, Victoria

For further information contact:

Daryl Nielsen

PO Box 821
Wodonga VIC 3689
Ph: (02) 6024 9650

Email: daryl.nielsen@csiro.au
Enquiries: cfe@latrobe.edu.au

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Photographer: Kyle Weatherman

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Author(s):   Stoffels[1,] R, Weatherman[2] K, Thiem[3] J, Butler[3] G, Morrongiello[4] J, Bond[2]
                             N, Koster[5] W, Keller Kopf[6] R, McCasker[6] N, Ye[7] Q, Zampatti[7] B and
                             Broadhurst[8] B

Author affiliation(s):   [1] National Institute of Water & Atmospheric Research Ltd, Christchurch,
                             NZ

                             [2] La Trobe University, Wodonga Vic.

                             [3] Department of Primary Industries, NSW

                             [4] University of Melbourne

                             [5] Department of Environment, Land, Water and Planning, Victoria

                             [6] Charles Sturt University, Albury NSW

                             [7] Department of Primary Industries and Regions, South Australia

                             [8] University of Canberra

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Executive summary

Background

To meet Basin Plan objectives and facilitate the Basin Wide Watering Strategy (Watering Strategy; MDBA 2014), scientists must tackle numerous challenges; three of which are particularly pressing. First, we must rapidly develop an understanding of how flow alteration interacts with climate change to affect biota within the Murray-Darling Basin (the Basin). Climate change imposes a form of 'non-stationarity' on flows management, in that the flow-ecology rules and decision problems formulated today will be altered by climatic change. This non-stationarity problem is explicitly recognised in the Watering Strategy.

Second, we must understand how biota respond to the flow-climate interaction at spatial and temporal scales most relevant to management. We need to be able to prioritise and plan environmental flows across multiple catchments within the Basin, and so require general models of ecological response.

Third, our understanding of how climate-flow interactions affect population processes at scales relevant to management must be captured in predictive ecological models. These models are required to: (a) forecast the ecological response to different decision options, leading to better-informed and more defensible environmental flow decisions; (b) facilitate defensible inferences concerning environmental flow impacts under a non-classical experimental design (without controls or replication); (c) improve our capacity to forecast the efficacy of flow management plans under a non-stationary environment; and (d) 'scale up' ecological responses to broader ecological extents or to river segments receiving environmental flows where data are absent or scarce.

Objectives and approach

We used long-term datasets spanning several rivers across the Basin to improve our predictive understanding of how the growth dynamics of two long-lived fishes—Murray cod (*Maccullochella peelii*) and golden perch (*Macquaria ambigua*)—respond to flow variability under a non-stationary climate. Individual growth rate may influence survival and recruitment and, therefore, may be a useful proxy for certain Basin Plan objectives. We had three objectives:

Objective 1 was to estimate growth-rate time series for Murray cod and golden perch in six catchments of the Basin using the information stored in otoliths (fish ear bone). Otoliths were analysed from the Gwydir, Lachlan, Murrumbidgee, Edward-Wakool, Goulburn and Lower Murray systems. Estimating the growth-rate history of an individual fish involves (Figure S 1): Step 1, capturing an individual, removing its otoliths, obtaining a slice through the middle of the otolith so that the width of annual growth rings or 'increments' are visible; Step 2, estimating the age of the individual at the time of capture; Step 3, starting from the outer edge of the otolith, measuring increment widths going back through time, such that we may then assign an increment width in an individual to a 'growth year' (1st Oct – 30th Sept) and a specific age (Figure S 1b). We assume that an individual has not made any large-scale (ca. > 200 km) movements during its lifetime when attempting to relate an individual's growth history to changes in flow and temperature at its place of capture.

Objective 2 was to model growth rates as a function of annual discharge and temperature. 'Annual discharge' was the mean discharge (ML/d) calculated across days of a 'growth year' (1st Oct – 30th Sept). 'Annual temperature' was the mean maximum air temperature calculated across days of the growth year. The modelling approach we used was particularly well suited to situations where inferences or predictions are sought at the population level or 'Basin scale' but where data are sampled from subsets of that population.

Objective 3 was to analyse uncertainty around the growth response to flow and temperature variability. Uncertainty pervades all forms of natural resource management. Improving our understanding of uncertainty around the effects of flows will, in turn, increase our understanding of the range of outcomes that may result from a decision, facilitating more defensible and effective decisions.
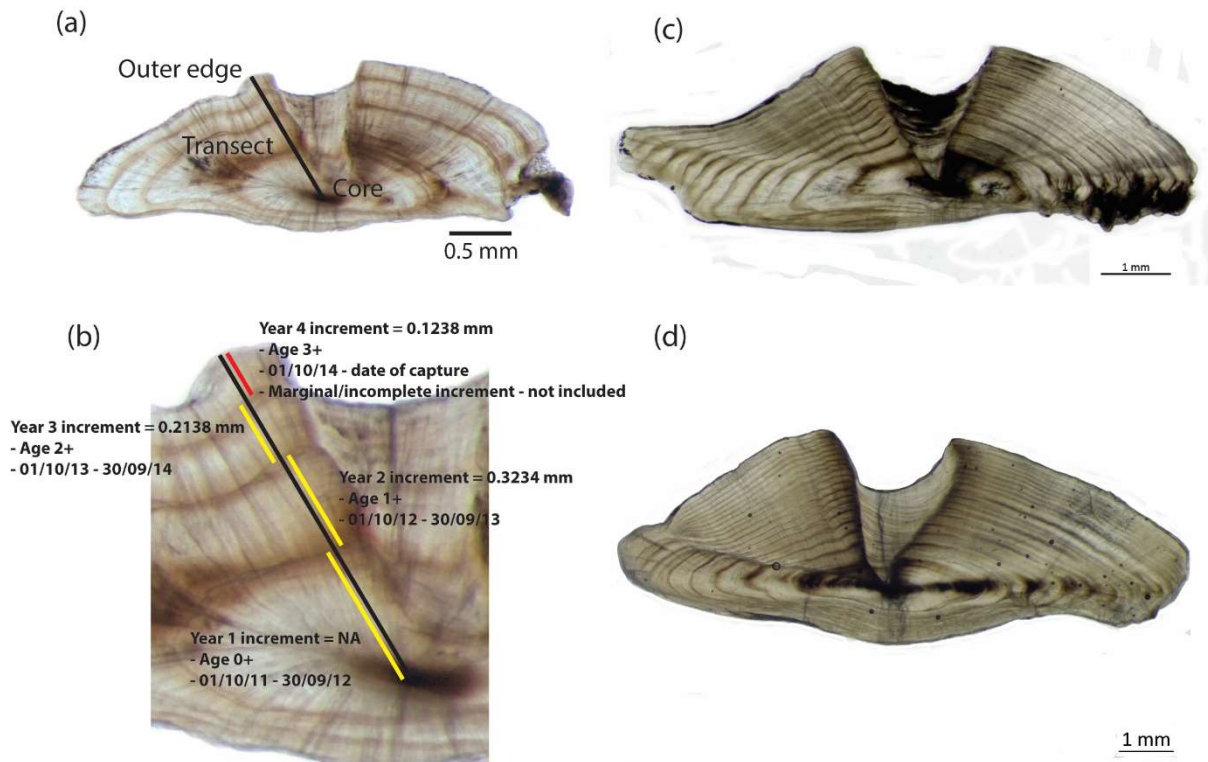
Figure S 1. Photographs showing how we may obtain the growth history of an individual fish from its otoliths. (a)–(b) Otolith section from a 3+ year-old Murray cod showing key features of otolith increment measurement. Each annual growth increment comprises a pair of translucent and opaque bands that are equal to one year of growth. Broader translucent bands correspond to higher growth periods during warmer months, followed by narrower opaque bands that correspond to lower growth periods during cooler months. Also shown are examples of otolith sections from older individuals: (c) Murray cod age 12+ and (d) golden perch age 19+.

Effects of annual discharge and temperature on fish growth

Otoliths from a total of 961 Murray cod and 436 golden perch were photographed and analysed. From these otoliths we measured the widths of 4124 and 1957 annual increments from Murray cod and golden perch, respectively. Each of these increments is a measure of the mean growth rate of an individual fish over a year. These sample sizes demonstrate the utility of the biochronology approach to assemble a time series rapidly.

We found no evidence for relationships between golden perch growth and either annual discharge or annual temperature. The most likely explanation for this result is that golden perch undergo significant large-scale movements during their lifetime, which violates the critical assumption stated under Objectives and Approach. There is growing evidence in the Basin for golden perch undergoing relatively large-scale movements during their lifetime.

Annual growth of Murray cod showed significant, age-specific responses to annual discharge and temperature. A visual summary of the key Murray cod results is presented in **Figure S 2**.
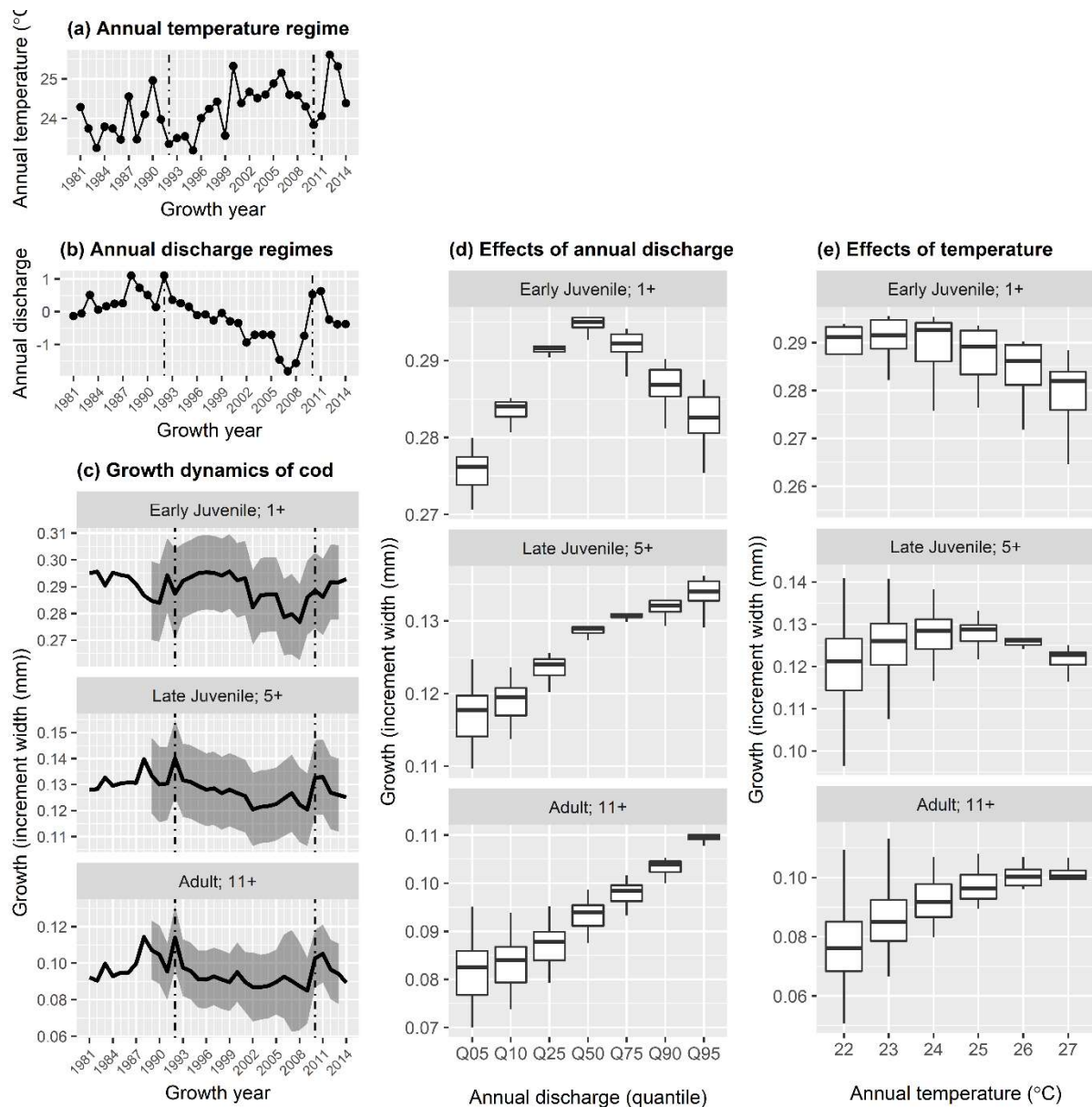
Figure S 2. Response of Murray cod growth to river flows and temperature - visual summary. Examples from the Murrumbidgee River are presented, but these examples are representative of the Basin as a whole. (a)–(c): Observed annual temperature and discharge time series, as well as the growth time series predicted by the final model (± 95% confidence interval) for different life-stages of Murray cod. Vertical dashed lines in (a)–(c) denote La Nina floods and predictions of growth without confidence intervals denote predictions beyond domain of covariates for this river. (d)–(e): predicted growth response to annual discharge (flow percentiles; e.g., Q50 is the median) and annual temperature (°C), respectively, of different life stages. Boxes present the uncertainty in the effect of a covariate (one of annual discharge or temperature) generated by the interaction that covariate has with temporal variation in the other covariate (see Methods).Growth of early juveniles (1+ and 2+) exhibited a unimodal relationship with annual discharge, peaking at the long-term median annual discharge. This is clearly seen in **Figure S 2d**, which presents predicted growth of Murray cod at seven quantiles of annual discharge (Q50 is the median annual discharge; Q25 is the

25th percentile, etc.). In lowland rivers, slackwaters may provide productive foraging habitat for fishes during early life history (Humphries *et al.* 2019), and the abundance of slackwaters peaks at intermediate discharges (Vietz *et al.* 2013). One mechanism driving this result may be that energy flow to early juvenile cod is highest at median flows when slackwater abundance peaks.

Contrasting with early juveniles, growth of late juvenile (3+ to 5+) and adult (> 5+) Murray cod increased with annual discharge, with the rate of increase being particularly high in adults (Figure S 2d). Higher annual discharge is associated with increased volume of foraging habitat and greater inundation of benches, floodrunners and other floodplain habitat, resulting in mobilisation of energy (McInerney *et al.* 2017). Looking at the time series Figure S 2c, we can see the strong positive effect of large floods on growth, but also how growth is depressed during the Millennium Drought (ca. 2000–2010).

Unimodal relationships between growth and annual temperature were evident across all Murray cod life stages. The annual temperature at which maximum growth occurred increased with age, such that growth was maximal at 23 °C, 24 °C and 26–27 °C in early juveniles, late juveniles and adults, respectively (Figure S 2e). The 'warming' of the thermal niche with age is commonly seen in both marine and freshwater fishes (Jobling 1996).

Importantly, an analysis of uncertainty clearly showed that the effects of each covariate—annual discharge and temperature—were robust to: (a) environmental uncertainty generated by the interaction one covariate had with stochastic temporal variation in the other, as well as spatial variation among rivers, and (b) statistical uncertainty generated by error in model parameter estimates.

Implications for management of riverine flows in the Basin, in a changing climate

Our study highlights the importance of flows of median annual discharge to growth of early juvenile Murray cod, likely because such flows increase the availability of slackwater habitat for profitable foraging. The distribution and abundance of slackwaters is a consequence of river-floodplain geomorphological dynamics. It follows that, on a decadal scale, the effects of managed flow regimes on the maintenance of vital geomorphological processes should be factored into long-term plans.

This research clearly highlighted the importance of high flows—floods in particular—to growth of late juvenile and adult Murray cod. Thus, our study both confirms and generalises the result of Tonkin et al. (2017). Increasing the frequency of floods would reduce the probability of hypoxic episodes (Kerr *et al.* 2013; Whitworth *et al.* 2012), while also promoting higher levels of fish productivity.

Given the stage-specific response of Murray cod growth to annual discharge, it is clear that no single level of annual discharge is optimal for Murray cod production. Interannual variability in flows must be maintained to promote production of Murray cod populations over the long-term, but noting we found no evidence for positive effects of annual discharge levels below the long-term median.

Following the IPCC, air temperature records up to 2006 are often used as a 'baseline' for evaluating climate change (IPCC 2013). Analysis of annual temperatures from our study systems during the baseline period showed that the mean annual temperature was 23.6 °C. This temperature coincided with peak growth of early juvenile cod. Indeed, the growth rate of early juveniles declined significantly with warming above the baseline annual temperature. Mean air temperatures are forecast to increase by as much as 5.3 °C by 2090 (CSIRO and Bureau of Meteorology 2015). Given the forecast rate of warming, we may expect depressed growth of juvenile Murray cod under climate change forecasts for the Basin. This may lead to reduced recruitment.

By contrast the data indicate that the warming forecast for the Basin may promote growth of adult Murray cod. Consequently, there is much uncertainty around the overall effect of warming scenarios on Murray cod populations in the Basin.

The Watering Strategy clearly states the need to quantify the threats posed by climate change. Our work shows that both droughts—through reduction of annual discharge—and warming pose a threat to Murray cod production.

Introduction

Background

To meet Basin Plan objectives and facilitate the Basin Wide Watering Strategy (Watering Strategy; MDBA 2014), scientists must tackle numerous challenges, three of which are particularly pressing (Stoffels *et al.* 2018).

First, we must rapidly develop an understanding of how flow alteration interacts with climate change to affect biota within the Murray-Darling Basin (the Basin). Even a cursory analysis of available air temperature data across the six catchments of the present study shows an alarming trend (Figure 1). Indeed, with reference to the Intergovernmental Panel on Climate Change's (IPCC 2013) Representative Concentration Pathways (RCPs), by 2090, increases in mean air temperatures within the Basin are forecast to be between 1.5 and 2.9 °C under RCP4.5 (low-emission, 'best-case' scenario; stabilising CO_2 at 540 ppm by end of 21st century), and 2.9 and 5.3 °C under RCP8.5 (high-emission scenario; CO_2 reaching 940 ppm by end of 21st century) (Ekström *et al.* 2015; Timbal *et al.* 2015; Watterson *et al.* 2015). River regulation in the Basin has greatly reduced the frequency and magnitude of floods (Sims *et al.* 2012) and by 2030 we may expect a further 13% decrease (cf. 2009) in total discharge under a 'medium-severity' climate forecast; a flow reduction approximating the volume of water set aside for a Sustainable Diversion Limit (SDL) within the Basin Plan (Kirby *et al.* 2013). Furthermore, the frequency and severity of droughts within the MDB are forecast to increase under climate change (CSIRO and Bureau of Meteorology 2015). Thus, climate change imposes a form of non-stationarity on flows management, with the flow-ecology rules and decision problems formulated today likely to be altered by climatic change. This non-stationarity problem—and the need to develop solutions—is explicitly recognised in the Watering Strategy (MDBA 2014).
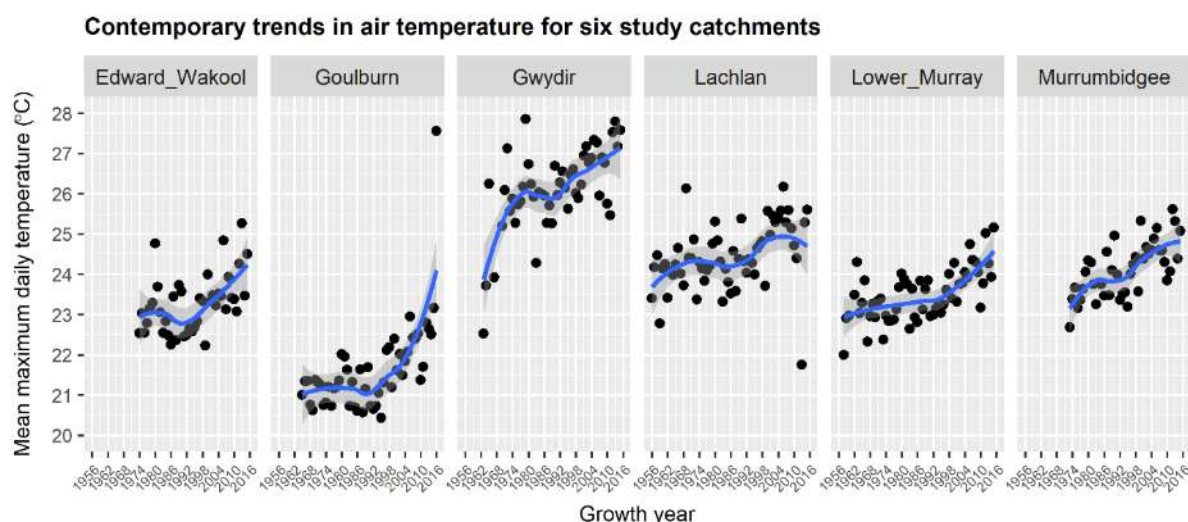
Figure 1. Annual mean maximum daily temperature is increasing throughout the Murray-Darling Basin. Shown are the time series of mean maximum daily temperatures for the six rivers studied here (including loess smooths +/- 95% CI).

Second, we must understand how biota respond to the flow-climate interaction at spatial and temporal scales most relevant to management. We need to be able to prioritise and plan environmental flows across multiple catchments within the Basin, and so require general models of ecological response; models that essentially treat river-specific responses to environmental flows as samples from the larger, Basin-wide 'population' of responses (Acreman & Ferguson 2010;

Arthington *et al.* 2010). With respect to the temporal scale of flow decision problems, managers seek answers to questions like: What is the impact on a population if it does not receive an overbank flow in 'x' years? For how long will the positive—or negative—impacts of a specific environmental flow persist on the population? To answer such questions, we need to improve our understanding of the temporal dynamics of riverine populations (Poff 2018; Stoffels *et al.* 2018; Tonkin *et al.* 2018).

Third, our understanding of how climate-flow interactions affect population processes at scales relevant to management must be captured in predictive ecological models. Stoffels et al. (2018) identified four major requirements for predictive models in flows management: (a) to forecast the ecological response to different decision options, leading to better-informed and more defensible environmental flow decisions (Polasky *et al.* 2011); (b) facilitating intervention analysis, hence defensible inferences concerning environmental flow impacts under a non-classical experimental design (without controls or replication; Stewart-Oaten & Bence 2001; Webb *et al.* 2010); (c) improving our capacity to forecast the efficacy of flow management plans under a non-stationary environment (Shenton *et al.* 2012; Wolkovich *et al.* 2014); and (d) 'scaling up' ecological responses to broader ecological extents or to river segments receiving environmental flows, but where data are absent or scarce (Ferrier 2011; Urban 2005).

In the present study, we use long-term data sets spanning several rivers across the Basin to improve our predictive understanding of how the growth dynamics of two long-lived fishes—Murray cod (*Maccullochella peelii*) and golden perch (*Macquaria ambigua*)—respond to flow variability under a non-stationary climate. Towards that end, we estimate growth-rate time series for cod and golden perch inhabiting six catchments of the Basin, using the information stored in otolith (fish ear bone) biochronologies.

Why fish; why growth?

Fish are recognised as a critical indicator of flow outcomes under the Basin Plan (Basin Plan 2012). A key objective within the Watering Strategy is to manage flows to improve survival rates of fishes with medium to long life-spans (MDBA 2014). If we wish to see increases in fish population size, then meeting this objective is critical. From a scientific perspective, however, direct estimation of flow-survival relationships is a great challenge, and takes several years of quality data to establish (Walters 1997). The impact of flows on fish survival in the Basin is being studied directly as part of the Commonwealth's Long-Term Intervention Monitoring Program (LTIM). To complement LTIM's direct, long-term analyses of flow-survival relationships at the Basin-scale, there is a need for further short-term studies that take novel approaches to the problem. For example, studies that improve our predictive understanding of how flows affect proxies of survival will enhance our ability to report on flow outcomes at the temporal scale of 1-5 years.

Individual growth rate may influence critical population processes (Sauer & Slade 1987) and so may be a useful proxy for the Basin Plan objectives of increased survival and recruitment. In certain long-lived fishes growth rate may be positively related to 0+ cohort strength (Dutterer *et al.* 2013; Jensen & Johnsen 1999; Nunn *et al.* 2007; Pitchford *et al.* 2005; Tanaka *et al.* 2006) and juvenile survival rates more generally (Sogard 1997; Vincenzi *et al.* 2012). Therefore, the growth rate of juveniles— which can be from cohorts 0+ through to 5+ in the Basin, depending on the species and environmental context—may be linked to rates of recruitment into the adult stage of life. Very little, if anything, is understood about how temporal variation in the growth rates of adults affects their rates of survival through time.

There are several reasons why we expect river flows to interact with water temperature to affect growth of long-lived native fishes of the Basin. These reasons, as well as literature to support our broad hypotheses, are presented in Table 1.

Table 1. Justification of our expectation that growth of large-bodied fishes of the Basin will be affected by both flows and temperature.

Flow or temperature variable	Hypothesised impact on environment and individual growth
High flow frequency, duration and/or magnitude	• Inundation of previously dry habitat, hence mobilisation of nutrients supporting ephemeral 'boom' in secondary production (increased macroinvertebrate production) (Baldwin *et al.* 2013; Cook *et al.* 2015; McInerney *et al.* 2017). • Increased habitat volume and diversity supporting secondary production (differs from above as we may not necessarily see increased production per unit area, just more area *per se*; e.g. foraging opportunities for juveniles in backwaters, on floodplain, etc.) (Benke 2001; Gallardo *et al.* 2008; Sheldon *et al.* 2002). • Provision of cues supporting movement, hence possible access to, and exploitation of, new foraging habitats, in both the longitudinal and lateral dimensions (David & Closs 2002; Koster & Crook 2008; Koster *et al.* 2014; Stoffels *et al.* 2015; Stoffels *et al.* 2014). • Hypothesised **increased growth** of fishes during years with more high flow days (Kelly *et al.* 2017; Limm & Marchetti 2009; Morrongiello *et al.* 2014; Peterson & Jennings 2007; Shephard & Jackson 2009; Tonkin *et al.* 2011).
Low flow frequency, duration and/or magnitude	• Logically, the inverse of the above mechanisms, and in addition: • Lower dissolved oxygen during very low flow periods, limiting aerobic scope, hence growth (Campbell & Rice 2014; McNatt & Rice 2004; Pichavant *et al.* 2001; Pichavant *et al.* 2000). • 'Beyond-optimal' temperature (too warm) during extreme low flows, decreasing growth (Portner & Knust 2007). • Hypothesised **decreased growth** of fishes during years with a high number of low flow days.
Frequency of favourable water temperatures	• Being ectotherms, fish growth is inextricably linked to temperature, with growth rates increasing to a thermal optimum (Jobling 1996; Kingsolver 2009; Neuheimer *et al.* 2011). • We anticipate that water temperatures between 20 and 30 °C will generally **promote growth** of Murray cod and golden perch (e.g. Morrongiello *et al.* 2011).
Frequency of days exceeding thermal optimum	• Growth does not increase with temperature indefinitely. Beyond a thermal optimum, growth rate of fishes will decline as warm water becomes physiologically stressful. • We anticipate **reduced growth** during years containing a high frequency of days exceeding 30 °C.

Objectives

We had three Objectives: Objective 1 was to estimate growth-rate time series for cod inhabiting five catchments of the Basin, using the information stored in otolith (fish ear bone) biochronologies. The dearth of quality time series of sufficient length is a major barrier to meeting the three aforementioned challenges (Best 2019; Clark *et al.* 2001; Shea *et al.* 1998). Use of biochronologies from certain hard parts of organisms provides a novel way of rapidly obtaining long time series (Morrongiello *et al.* 2012).

Objective 2 was to parameterise and select mixed-effects additive models for inference and prediction. Drivers of growth dynamics over large spatial scales are typically a complex mix of 'intrinsic' and 'extrinsic' factors (Morrongiello & Thresher 2015). In our case, intrinsic sources of variance in growth essentially refer to the influence of phenotype and genotype; the effects of age and the individual. Extrinsic sources of variance in growth refer to environmental covariates that vary in space and time; flow and temperature are of primary interest but, to facilitate general, population-wide inference, we take into account the effect of river system on the sub-populations studied. Mixed-effects models are particularly well suited to data where individual observations exhibit correlations at multiple, hierarchical levels, and where inferences or predictions are sought at the population level, but where data is sampled from subsets of that population (Pinheiro & Bates

2000). Such models have been used to great effect to draw inferences from highly structured growth rate data (Morrongiello *et al.* 2011; Tonkin *et al.* 2011; Weisberg *et al.* 2010). We extend that approach here to the use of additive models (Wood 2017), allowing us to better understand the more complex, nonlinear responses of growth to extrinsic covariates (also see Rountrey *et al.* 2014).

Objective 3 was to use the output of Objective 2 to analyse uncertainty around the growth response of Murray cod to flow variability. Uncertainty pervades all forms of natural resource management. Improving our understanding of uncertainty around the effects of flows will, in turn, increase our understanding of the range of outcomes that may result from a decision and facilitate more defensible and effective decisions (Conroy & Peterson 2013). We determined the relative contribution of environmental and statistical uncertainty around the growth predicted to result from flow variation. Specifically, we estimated uncertainty in the predicted effect of annual discharge on growth generated by (a) temporal stochasticity in annual temperatures, noting growth dynamics of fishes are likely driven by an interaction between flow and temperature regimes; and (b) both temperature uncertainty and uncertainty contributed by error around model parameters. Following Conroy and Peterson (2013), these are special cases of environmental and statistical uncertainty, respectively. Given river managers also wish to better understand the possible effects of climate change on ecological assets (e.g., Murray cod), we also repeated the above uncertainty analysis but focusing on temperature impacts against a background of flow variability. Last, we determined how consistent flow and temperature effects are across catchments, noting that spatial context-dependencies comprise another form of environmental uncertainty around flow outcomes.

Methods

Data collation

Full descriptions of data collation and measurements for (a) otoliths and (b) air and temperature data are provided in Appendices 1 and 2, respectively.

Otoliths from Murray cod were obtained from five regulated river systems within the Murray-Darling Basin: The Gwydir, Lachlan, Murrumbidgee, Edward-Wakool, Goulburn and Lower Murray systems. Collections were made from a river segment ca. 100-400 km in length within each river system. Having obtained a photograph of the sagittal section of each otolith, photographs were imported into Zen 2.3 Blue Edition (Carl Zeiss Microscopy GmbH, 2011) microscopy software for precise digital measurements. The widths of annual growth increments were measured perpendicular to the axis of growth along a transect line that was established on the proximal axis, drawn from the core to the outer edge (following Morrongiello *et al.* 2011). Fish were assigned a nominal birthdate of October 1st and annual growth increments were assigned 'growth year' t (such that growth year is 01/10/t to 30/09/t+1) by back-calculation from the capture date.

Daily discharge (ML d^{-1}) data were obtained from 18 gauges (Table A 2). Air temperature was used as a surrogate for water temperature due to the paucity of water temperature logging stations throughout the MDB (Table A 2). Air temperatures were paired with a discharge gauge by selecting the climate logging station closest to the discharge gauge.

We did not have information about the movement history of individuals within river systems so we made no attempt to pair individual otoliths with individual gauges at a fine spatial resolution. Instead, for each of the six river systems we generated a daily discharge time series that applies to each system as a whole. As such, any inference concerning the effects of discharge on growth pertains to mean flows moving through the system as a whole, not individual reaches or anabranches, for example (Appendix).

Model parameterisation, selection and testing

Prior to the calculation of any hydrological covariate, all time series of mean daily discharge were transformed into standard, log-normal random deviates (Wackerly *et al.* 2002). This allowed us to take discharge distributions from rivers with very different means and standard deviations, and give them the same location (zero) and standard deviation (one). Distributions of discharges for our study rivers were clearly log-normally distributed, such that the locations of standardised series were closer to zero when using log-normal random deviates than normal random deviates. Parameters for the transformation (means and standard deviations of *ln*(x+1) daily discharge values for each gauge) were obtained using all available discharge records for each gauge (Appendix B). Discharge standardisation was carried out prior to obtaining system-level mean series.

The general modelling approach employed was mixed-effects regression, used to account for correlation among observations within various groups at multiple levels in the data (Pinheiro & Bates 2000). For any individual fish, increment width (G; mm) was used as an index of growth for that growth year (Morrongiello & Thresher 2015). The intrinsic drivers of growth included both fixed and random terms. Age (A) was a fixed term—noting ontogenetic niche shifts are strong in fishes (Werner & Gilliam 1984)—while individual enters the formulae as a random term, acknowledging that any response of growth to other factors is likely to be correlated within individuals.

For this analysis we sought model parameterisations of extrinsic factors that captured how coarse interannual changes in the flow and thermal state of rivers drive growth dynamics of Murray cod and golden perch. Three flow and three temperature covariates were identified as candidates, following exploratory graphical analyses testing for possible relationships with growth. Appendix C describes these covariates and the mechanisms by which they may affect fish growth. Statistical models containing collinear covariates can lead to spurious inferences and forecasts (Wood 2017; Zuur *et al.* 2009), so we screened the possible covariates for collinearity, leaving two (0): mean annual standardised discharge in growth year t (F_t; hereafter 'annual discharge'), and annual mean maximum daily air temperature (T_t; hereafter 'annual temperature').

Prior to fitting models to data, we graphically examined relationships between annual discharge, annual temperature and growth at different ages in each river. We did this to ensure that some relationships between growth and covariates were evident prior to any model fitting. This step of our analysis indicated relationships between covariates and Murray cod growth were clear and likely quite strong. By contrast, no patterns were evident in the golden perch data—we could not see any evidence for relationships between covariates and golden perch growth at any level in the data. Consequently, further formal analysis of the golden perch data set was not carried out.

Graphical examination of the relations between covariates and Murray cod increment widths showed that nonlinear relations were common. These nonlinear relationships had forms that were unlikely to be neatly described by low-order polynomial terms (e.g., quadratics), especially in the multilevel context, where parameters of, say, quadratic terms were likely to vary among levels of random factors. In light of these observations we chose to use Generalised Additive Mixed Models (GAMMs; Wood 2017) for modelling G as a function of covariates.

The set of ten candidate GAMMs is described in Table 2. The candidate model set was mostly nested, such that simpler models are subsets of more complex models. There were three classes of model, each of which partitioned different components of variance in G: (1) Null models isolating the contributions of intrinsic factors individual and age, and the sole, extrinsic impact of river system on G; (2) four models that now add the extrinsic factors of primary interest in this paper—effects of annual discharge and temperature; (3) as for (2), but now including temporal autocorrelation in G (Table 2).

Table 2. Description of the three classes of Generalised Additive Mixed Models fitted to increment width data.

Model name	Formula	Description
Spatial and intrinsic effects		
Null 1	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + \varepsilon_{tij},$ $j = 1, \dots, n, \quad i = 1, \dots, n_j, \quad t = 1, \dots, n_{ij}$ $\alpha_j \sim N(0, \sigma_1^2), \quad \alpha_{ij} \sim N(0, \sigma_2^2), \quad \varepsilon_{tj} \sim N(0, \sigma^2).$	Increment width (G_{tj}; mm) of individuals during growth year t within river system j is a function of population-level mean growth rate (α) + deviation induced by River j from population mean (α_j) + deviatioin induced by effect of Individual i within River j (α_{ij}) + error. The factors α is fixed while α_j and α_{ij} are random. The number of rivers, n, is 5, while n_j is the number of growth years in the data set within River j, and n_{ij} is the number of growth years from Individual i within River j.
Null 2	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + \varepsilon_{tij},$ $j = 1, \dots, n, \quad i = 1, \dots, n_j, \quad t = 1, \dots, n_{ij}$ $\alpha_j \sim N(0, \sigma_1^2), \quad \alpha_{ij} \sim N(0, \sigma_2^2), \quad \varepsilon_{tj} \sim N(0, \sigma^2).$	As above, but now containing a smoother, f, for the effect of the age during year t of individual i in River j. Age is a fixed factor.
Spatial, intrinsic and extrinsic effects		
E1	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + f(F_{tij}, A_{tij}) + \varepsilon_{tij},$ $j = 1, \dots, n, \quad i = 1, \dots, n_j, \quad t = 1, \dots, n_{ij}$ $\alpha_j \sim N(0, \sigma_1^2), \quad \alpha_{ij} \sim N(0, \sigma_2^2), \quad \varepsilon_{tj} \sim N(0, \sigma^2).$	Null 2 + curvilinear effects induced by the interaction standardised discharge has with age.
E2	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + f(T_{tij}, A_{tij}) + \varepsilon_{tij},$ $j = 1, \dots, n, \quad i = 1, \dots, n_j, \quad t = 1, \dots, n_{ij}$ $\alpha_j \sim N(0, \sigma_1^2), \quad \alpha_{ij} \sim N(0, \sigma_2^2), \quad \varepsilon_{tj} \sim N(0, \sigma^2).$	Null 2 + curvilinear effects induced by the interaction mean maximum daily temperature has with age.
E3	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + f(F_{tij}, A_{tij}) + f(T_{tij}, A_{tij}) + \varepsilon_{tij},$ $j = 1, \dots, n, \quad i = 1, \dots, n_j, \quad t = 1, \dots, n_{ij}$ $\alpha_j \sim N(0, \sigma_1^2), \quad \alpha_{ij} \sim N(0, \sigma_2^2), \quad \varepsilon_{tj} \sim N(0, \sigma^2).$	Null 2 + the curvilinear effects of the interaction standardised discharge has with age, and the interaction between age and mean maximum daily temperature. There is no three-way interaction between age, standardised discharge and temperature, so the shape or curvature of the age-specific relationship between one extrinsic covariate and growth is assumed constant over the other extrinsic covariate.
E4	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + f(F_{tij}, A_{tij}) + f(T_{tij}, A_{tij}) + f(F_{tij}, T_{tij}, A_{tij}) + \varepsilon_{tij},$ $j = 1, \dots, n, \quad i = 1, \dots, n_j, \quad t = 1, \dots, n_{ij}$ $\alpha_j \sim N(0, \sigma_1^2), \quad \alpha_{ij} \sim N(0, \sigma_2^2), \quad \varepsilon_{tj} \sim N(0, \sigma^2).$	As E3, but now allowing for three-way interaction between age, standardised discharge and temperature. The shape or curvature of the age-specific relationship between one extrinsic covariate and growth is allowed to vary over the other extrinsic covariate.
Spatial, intrinsic and extrinsic effects, including temporal autocorrelation		

E5-E8	Formulae E5-E8 follow E1-E4, respectively, but with a first-order correlation structure of residuals across growth years, such that: $$\text{cor}(\varepsilon_s, \varepsilon_t) = \begin{cases} 1 & \text{if } s = t \\ \rho^{|t-s|} & \text{else} \end{cases}$$	Descriptions as for E1-E4, now with temporal autocorrelation.

The last class of models was parameterised to account for temporal autocorrelation amongst residuals, as significant temporal autocorrelation can (a) affect inferences if unaccounted for (Zuur *et al.* 2009) and (b) be interesting inasmuch as it indicates there may be multi-year biological processes unfolding that are unaccounted for within the fixed components of models.

The mgcv package was used for all additive modelling (Wood 2017). Generalised cross-validation was implemented to ensure individual smooth terms were not overfitted to data. We used an information-theoretic approach for model selection (Burnham & Anderson 2002), noting that use of cross-validation for selecting mixed-effects models is problematic (Wang & Gelman 2015). An objective of this analysis was to yield general inferences and predictions concerning how Murray cod growth responds to discharge and temperature. Towards that end we tested the predictive accuracy of the final GAMM using independent data; data not used to estimate parameters. Model selection was carried out using ca. 80% of the global data set (the training data), reserving the remaining ca. 20% of the data for model testing (the testing data). We wished to test the accuracy of predictions about how individual fish respond to discharge and temperature, so we ensured no 'leakage' of data from individual fish across testing and training data sets (using groupdata2; Olsen 2017). Nash-Sutcliffe Efficiency (NSE; Nash & Sutcliffe 1970)—which is essentially the coefficient of determination estimated using the testing data—was used to determine predictive accuracy. NSE measures how close the observed and predicted values within the testing data are to the 1:1 line. NSE values range from −∞ to 1. An NSE of 1 corresponds to a perfect match between predictions and the observed data, an NSE of 0 indicates that the model predictions are as accurate as the mean of the observed data; and an NSE less than 0 indicates that the observed mean is a better predictor than the model.

Analysis of final model and uncertainty

When analysing mixed-effects/hierarchical models it can be difficult to acquire a full understanding of (a) the direction and magnitude of individual covariate effects; and (b) sources of uncertainty concerning those effects, through a casual examination of coefficients and the fitted model alone (Gelman & Hill 2007). This may be particularly true in the context of GAMMs, where more complex nonlinear responses may result from interactions among several variables. Following Gelman and Hill (2007), we used simulation to answer the following questions:

1. What is the relationship between growth and annual discharge across ages, and how much uncertainty in that relationship is generated by (a) variation in annual temperature among years; and (b) both variation in annual temperature among years and uncertainty in the value of GAMM parameters?

2. What is the relationship between growth and annual temperature across ages, and how much uncertainty in that relationship is generated by (a) variation in annual discharge among years; and (b) both variation in annual discharge among years and uncertainty in the value of GAMM parameters?

3. How consistent are answers to the above two questions across rivers?

Two fixed, extrinsic covariates were the focus of this analysis: annual discharge and annual temperature. At its core the algorithm basically involves predicting growth of Murray cod at a set of

fixed values of one of these covariates while simulating environmental uncertainty (plus statistical uncertainty) in the other covariate. The output of this analysis was a set of boxplots describing distributions of predicted Murray cod growth rates. For each of 5 rivers and 3 ages (see Results) we generated 2 (forms of uncertainty) × p (levels of a fixed, extrinsic covariate) = $2p$ individual boxplots (an individual box, two whiskers, etc.). Thus we generated $5 × 3 × 2 × p = 30p$ individual boxplots for both annual discharge and temperature.

For annual discharge we determined the distributions of predicted growth rates for $p = 7$ levels, hence $2 × 7 = 14$ boxplots per river-age pairing. These seven levels of annual discharge were defined by the following percentiles of the domain of annual discharge values in the training data set: 5; 10; 25; 50; 75; 90; 95%.

For annual temperature we determined the distributions of predicted growth rates for $p = 6$ levels, hence $2 × 6 = 12$ boxplots per river-age pairing. These six levels of annual temperature were defined by the integer sequence 22, 23,…,27 °C. The first and last value of this sequence (22 °C and 27 °C) were approximately the 10th and 90th percentiles, respectively, of the temperature data in the training set.

The Appendix explains this analysis in detail.

Results

Otoliths from a total of 961 Murray cod and 436 golden perch were photographed and analysed. From these otoliths we measured the widths of 4124 and 1957 annual increments from Murray cod and golden perch, respectively. Each of these increments is a measure of the mean growth rate of an individual fish over a year. We obtained insufficient Murray cod otoliths from the Lower Murray to include that river system in the Murray cod analysis. Further information about the otolith database can be found in the Appendix.

Given the data and the set of candidate models, Model E8 was by far the most likely model of Murray cod growth dynamics, with an Akaike weight of one (Table 3). The four models that included temporal autocorrelation of growth were the four most likely models in the candidate set. The null models were the least likely models in the candidate set (Table 3).

Table 3. Performance statistics for the models in the candidate set. Models sorted in increasing order by their Akaike Information Criteria (AIC; decreasing log-likelihood (Log(L)). $\Delta_i = AIC_i - min(AIC)$ is the AIC model rank; and w_i is the Akaike weight of model i, interpreted as the approximate probability that model i is the best model in the candidate set (Burnham and Anderson 1998).

Model name	AIC	log(L)	Δ_i	w_i
E8	-13898.96	6967.48	0.00	1.00
E7	-13834.60	6928.30	64.36	0.00
E5	-13799.87	6908.93	99.10	0.00
E6	-13735.69	6876.84	163.28	0.00
E3	-13651.81	6835.91	247.15	0.00
E1	-13583.60	6799.80	315.36	0.00
E2	-13479.31	6747.65	419.66	0.00
E4	-13472.38	6753.19	426.59	0.00
Null 2	-13440.59	6726.29	458.38	0.00

| | Null 1 | -8004.02 | 4006.01 | 5894.94 | 0.00 |

The fixed terms of Model E8 included a global intercept, and four smooth terms: (1) the effect of age; (2) the interaction between age and annual discharge; (3) the interaction between age and temperature; and (4) the interaction between age, annual discharge and temperature (Table 2). There was weak evidence for a significant effect of the third smooth (F = 0.57; P = 0.72), so that term was dropped from Model E8 to yield the final model, presented in Table 4 (AIC = -13897; log(L) = 6966). This final model fit the data very well, with generally homogeneous residuals and no bias evident in the fit (Appendix). Predictive accuracy, as measured using NSE, was 0.79, which was comparable with the variance explained in the training data by the model (Table 4).

One of the most notable features of the final model's random component is the high temporal autocorrelation among residuals through time. The estimated value of ρ was 0.49, meaning that, after we take into account the variance explained by our flow and temperature covariates, there is residual variation in cod growth that is significantly correlated among years (Table 4). Residual increment widths in Year t and t-1 have a correlation of 0.49; residual increment widths in Years t and t-2 have a correlation of $0.49^2 = 0.24$, and so on.

Table 4. Parameter estimates of the final model of Murray cod growth.

Murray cod				
$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + f(F_{tij}, A_{tij}) + f(F_{tij}, T_{tij}, A_{tij}) + \varepsilon_{tij}$				
$j = 1, \ldots, n, \quad i = 1, \ldots, n_j, \quad t = 1, \ldots, n_{ij}$				
$\alpha_j \sim N(0, \sigma_1^2), \quad \alpha_{ij} \sim N(0, \sigma_2^2), \quad \varepsilon_{tj} \sim N(0, \sigma^2)$		$\text{cor}(\varepsilon_s, \varepsilon_t) = \begin{cases} 1 & \text{if } s = t \\ \rho^{\lvert t-s \rvert} & \text{else} \end{cases}$		
$R^2 = 0.82$		NSE = 0.79		
Fixed parameters:				
Parametric coefficient:				
	Estimate	SE	t	P
Intercept, α	0.185	0.007	26.73	<0.001
Approximate significance of smooth terms:				
	edf	F	P	
$f(A_{tij})$	8.775	98.271	< 0.001	
$f(F_{tij}, A_{tij})$	6.103	5.114	0.003	
$f(F_{tij}, T_{tij}, A_{tij})$	7.801	18.718	< 0.001	
Random parameters:				
σ_1	σ_2	σ	ρ	
0.0152	0.0001	0.0323	0.4954	

Continuing with the random component of the model, variation in intercepts among individuals within rivers was low, but variation in intercepts among rivers was approximately half that of residual error (Table 4). Calculating the intraclass correlation coefficients (Pinheiro & Bates 2000) for Murray cod, the correlation in growth among individuals within rivers was 0.32, while correlation in increment widths within individuals within rivers was also 0.32.

Considering the sampled population as a whole, age accounted for most of the variation in annual growth; growth rate declines with age (Table 4; Appendix). Indeed, the global R^2 of the model including only spatial and intrinsic effects or age and individual (Null 2) was 0.80, while that of the final model was 0.82 (Table 4). Nevertheless, the extrinsic flow and temperature covariates still had significant effects on growth (Table 4).
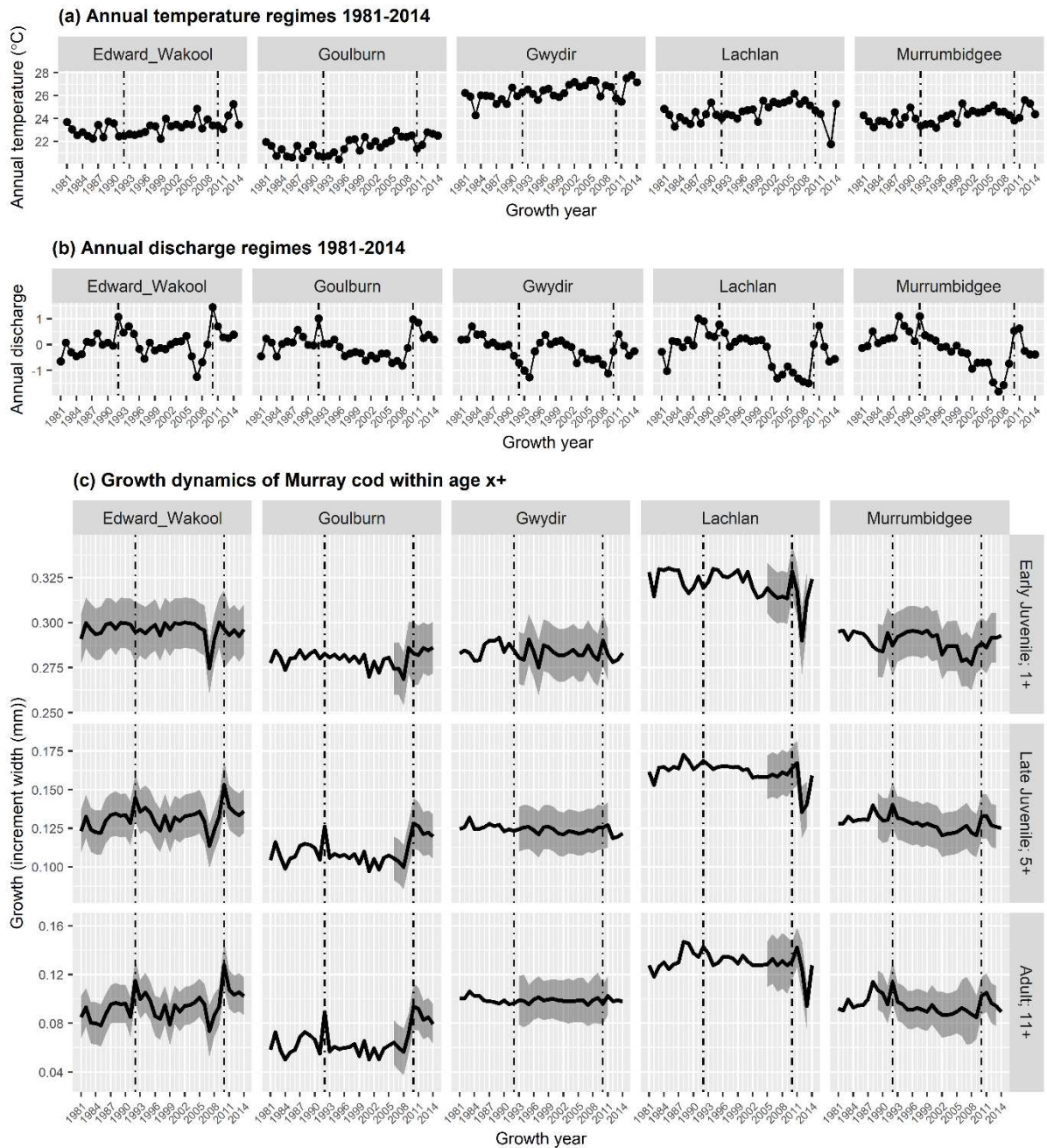
Figure 2. Observed time series of annual temperature and discharge and fitted time series of Murray cod growth for five rivers in the Basin. Observed time series of annual temperature (a) and discharge (b) within the global domain of the training data set. Vertical dashed lines denote timing of La Nina floods. Long-term median discharge denoted by y = 0 in (b). The fitted model (+ 95% CI) is presented (c) and model predictions beyond the temporal domain of river-specific data sets are also presented (where there is a line but no CI). Model fits/predictions are presented for 1+, 5+ and 11+ individuals. Model fits include random effects of rivers, as well as the fixed, population effects.

The impacts of annual discharge and temperature were clearly age-specific (Appendix). Differences in response among age were most noticeable between early juvenile (ca. 1+ to 2+), late juvenile (ca. 3+ to 5+) and adult (> 5+) stages (0). For ease of interpretation, subsequent analysis, figures and discussion are presented in the context of these three stages.

Figure 2 presents the fitted model, including the random effects of individual rivers (**Figure 2**c). Model predictions are extended beyond the temporal domain of the data in all rivers but the

Edward-Wakool, where growth data extended from 1981-2014 (Figure 2c; Appendix A). The observed time series of annual temperatures and discharges are also presented across the global temporal domain of the training data (Figure 2a, b). The period 1981-2014 encompassed droughts and floods, notably two La Nina floods (vertical dashed lines in Figure 2) and the Millenium Drought ca. 2000-2010 (Bond *et al.* 2008). In addition to interannual stochasticity in annual temperatures, a warming trend can be seen in **Error! Reference source not found.**a across all rivers, within the global domain of our training data set. Strong variation in annual discharge was observed within the domain of our training data (Figure 2b). In addition to the large La Nina floods, there was a chronic reduction in annual discharge during the Millennium Drought across all rivers (Figure 2b).

The fitted growth model highlights the stage-specificity of Murray cod growth dynamics and some clear effects of annual discharge that are consistent across rivers. For late juveniles and adults, growth rates are reduced during drought but increase sharply during floods; the effect of the La Nina floods is most evident (Figure 3). Floods have a particularly strong positive effect on growth of adults (Figure 3c). Early juvenile growth is suppressed when annual discharge departs strongly from the long-term median; this effect is strongest when annual discharge drops below the median (Figure 3c).

With respect to the predicted effect of annual discharge on growth, Figure 3 shows that uncertainty generated by the interaction flow has with temperature stochasticity is small relative to that generated by statistical uncertainty. This is the case across all life stages and rivers (Figure 3). Despite the combined contributions of both environmental and statistical uncertainty, there was strong variation in the predicted growth among annual discharge levels, as indicated by strong separation of growth interquartile ranges (IQRs) within rivers (Figure 3).

Growth of early juvenile Murray cod peaks at intermediate annual discharge (50th percentile or median of annual discharge; Figure 3; top row). This unimodal response of early juvenile growth to annual discharge was consistent across rivers (Figure 3; top row). Growth of late juvenile and adult Murray cod increases with annual discharge (Figure 3; rows 2 and 3). Unlike the response of early juveniles, the slope and—in one river—the shape of the response varied among rivers. Within the Gwydir River, growth of late juvenile and adult Murray cod exhibited no clear response to annual discharge (Figure 3). In the other four rivers, late juvenile and adult growth increased with annual discharge, but the slope of the increase was notably different among rivers (Figure 3). Mean growth rates of all life-stages varied among rivers (Figure 3).
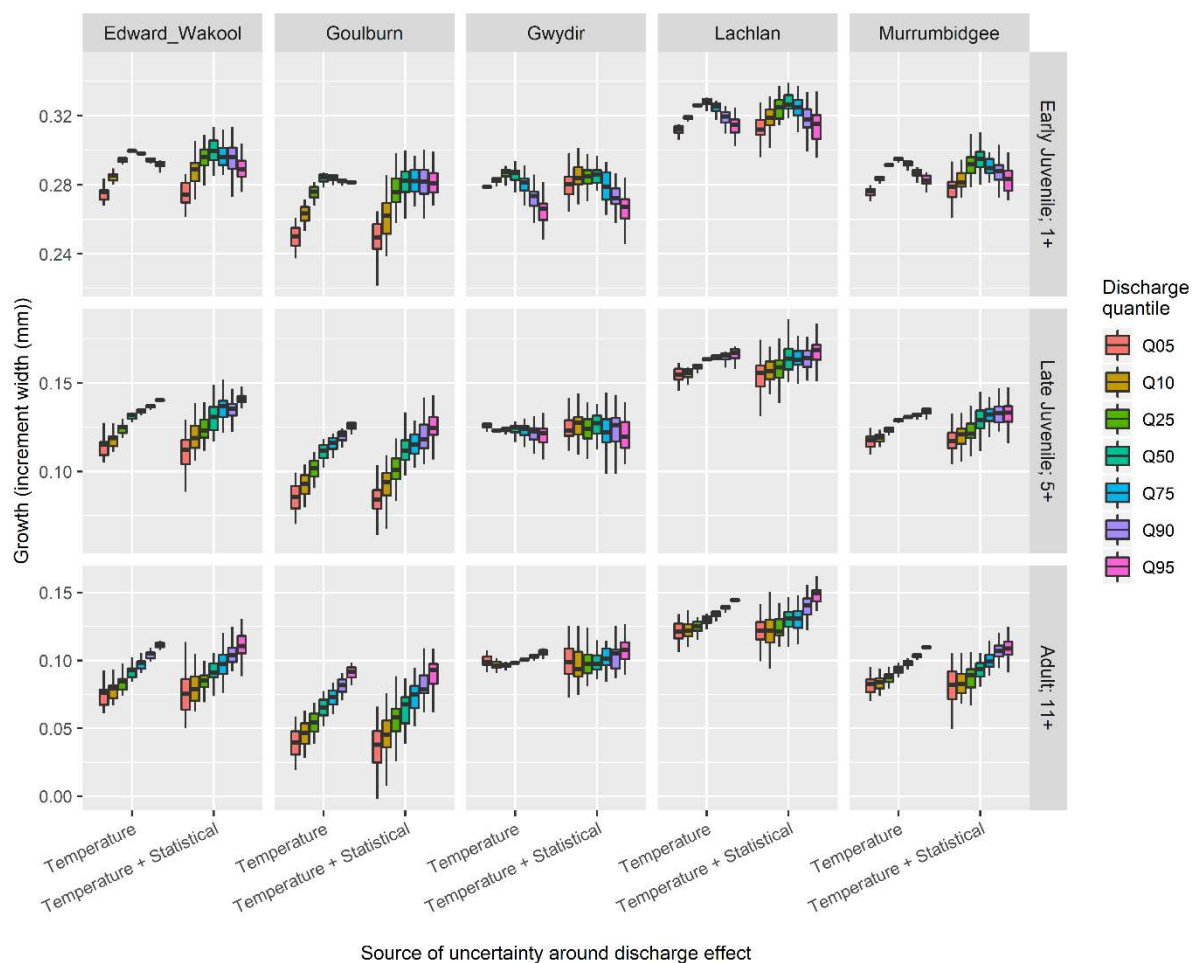
Figure 3. Stage-specific effects of annual discharge on Murray cod growth. Stage-specific effects of annual discharge on the growth of Murray cod, incorporating uncertainty in those effects due to the interaction annual discharge has with interannual variability in annual temperature ('Temperature'; a form of environmental uncertainty), and environmental and statistical uncertainty ('Temperature + Statistical'). Annual discharge quantiles determined using the training data set. Lower and upper hinges of boxes correspond to the 25th and 75th percentiles, while the horizontal line in the box indicates the median; whiskers extend to the lowest datum within 1.5 x the IQR above or below hinges.
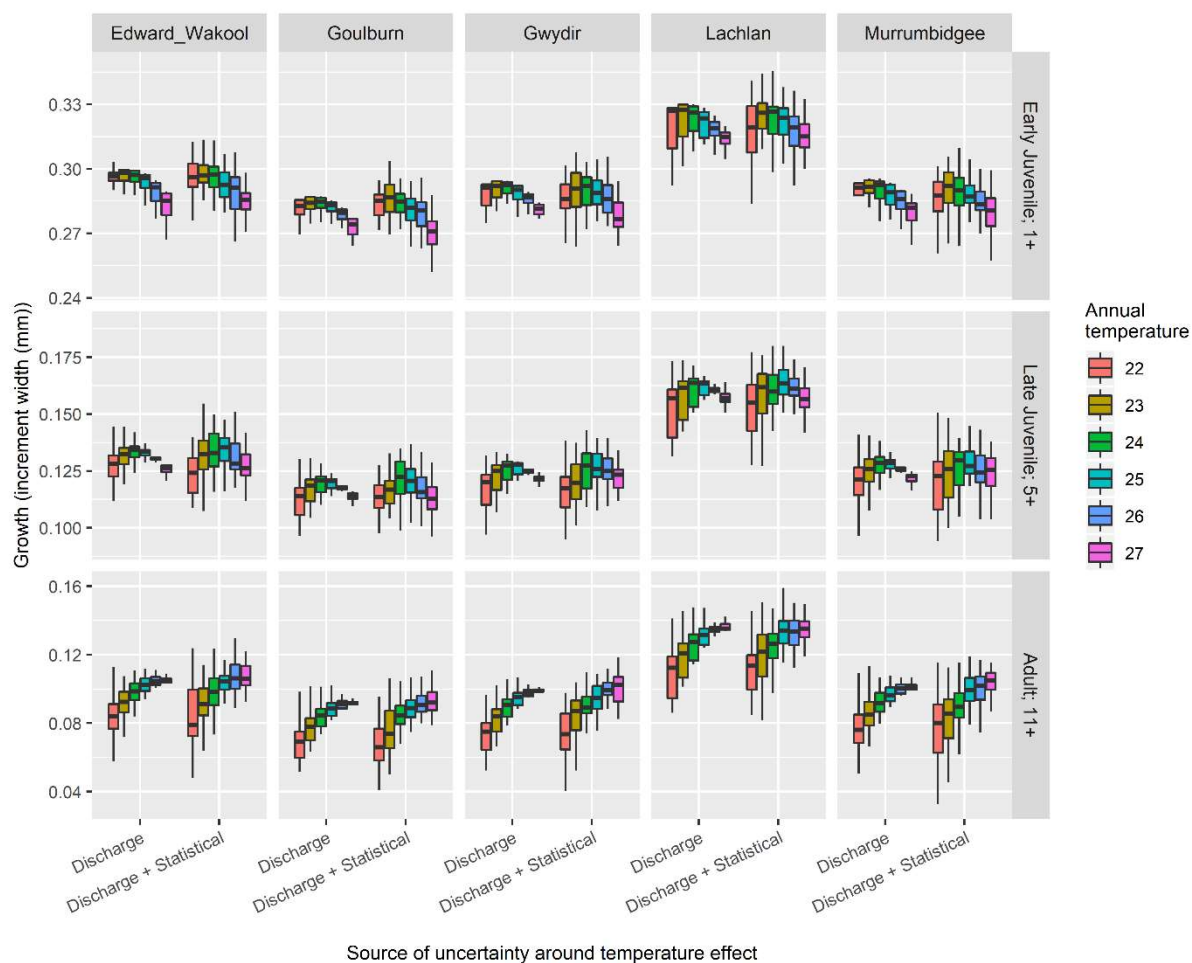
Figure 4. Stage-specific effects of annual temperature on Murray cod growth. Stage-specific effects of annual temperature on the growth of Murray cod, incorporating uncertainty in those effects due to the interaction annual temperature has with interannual variability in annual discharge ('Discharge'; a form of environmental uncertainty), and environmental and statistical uncertainty ('Discharge + Statistical'). Annual temperatures are in degrees Celsius. Lower and upper hinges of boxes correspond to the 25th and 75th percentiles, while the horizontal line in the box indicates the median; whiskers extend to the lowest datum within 1.5 x the IQR above or below hinges.

The effects of annual temperature on growth, as well as the contributions of different forms of uncertainty, were very consistent across rivers (Figure 4). At high annual temperatures, most of the uncertainty around the effect of temperature on growth was generated by statistical uncertainty (Figure 4). At lower annual temperatures, however, the interaction annual temperature has with variability in annual discharge often generated as much, or more, uncertainty in predicted growth as statistical uncertainty (Figure 4).

Despite high levels of statistical uncertainty concerning the effects of annual temperature on Murray cod growth, a clear pattern was evident: the temperature at which peak growth occurs increases with age (Figure 4). The annual temperature corresponding with peak growth was predicted to be approximately 23 °C, 24 °C and 26-27 °C in 1+, 5+ and 11+ individuals, respectively (Figure 4).

Discussion

Annual growth of cod showed significant, nonlinear, age-specific responses to an interaction between annual discharge and temperature. Growth of early juveniles (1+ and 2+) exhibited a unimodal relationship with annual discharge, peaking at the long-term median annual discharge. Growth of late juveniles (3+ to 5+) and adults (> 5+) increased with annual discharge in a linear fashion. Unimodal relationships between growth and annual temperature were evident across all life stages. The temperature at which maximum growth occurred increase with age, such that growth was maximal at 23 °C, 24 °C and 26-27 °C in early juveniles, late juveniles and adults, respectively. An analysis of uncertainty showed that inferences concerning the effects of each covariate on its own—annual discharge and temperature—were robust to uncertainty generated from environmental and statistical sources. As annual temperature increases, the data and model indicate that effects of annual discharge on growth are dampened across all life-stages.

The results of this analysis have implications for the management of river flows under a non-stationary climate. However, before we discuss those implications, the best model of Murray cod annual growth revealed stage-specific effects of flow and temperature variation. These effects need biological interpretation; given our understanding of river-floodplain ecosystems, what mechanisms might underpin the patterns in the data? Are patterns suggested by the best model consistent with our biological understanding of the system? We offer some answers to these questions below, noting that our answers should be treated as hypotheses.

The ontogeny of flow and temperature impacts

The unimodal relationship between annual discharge and growth of cod during the early juvenile stage was surprisingly strong and consistent across rivers, yet to our knowledge, this relationship has not been reported in any other riverine fish. As such, the mechanisms underpinning this relationship have not been investigated. Nevertheless, we offer the following hypotheses to explain the pattern: (a) slackwaters represent the most productive foraging habitat for cod during the early juvenile stage; and (b) slackwater area exhibits a unimodal relationship with river flows, peaking at median annual discharge. There is at least some support for both of these hypotheses in the literature.

Slackwaters are hydraulic 'microhabitats' within 'channel units' (following Fausch *et al.* 2002) characterised by shallow depths and low velocities (Vietz *et al.* 2013). Slackwaters are productive foraging habitats for riverine fishes during their early life history (Humphries *et al.* 2019). This may be at least partly due to slackwaters supporting high densities of micro- and macro-invertebrates (Ning *et al.* 2010). Although we know little about ontogenetic diet shifts in Murray cod (Stoffels 2013), micro- and macro-invertebrates generally comprise the most important source of energy for carnivorous riverine fishes during early ontogeny (Wainwright & Richard 1995; Winemiller 1989).

Price et al. (2012) showed that the surface area of slackwater habitat in the main channel of a lowland river is eroded at high flow rates. Vietz et al. (2013) reported a unimodal relationship between in-channel flow rate and the area of slackwater habitat in a lowland river. Thus the unimodal relationship between early juvenile growth and annual discharge may be a consequence of a similar relationship between annual discharge and slackwater surface area.

In contrast with early juveniles, growth of late juvenile and adult Murray cod increased in a mostly linear manner when annual temperatures are below 26 °C. This result may indicate that slackwater microhabitats, and/or the micro- and macro-invertebrates they support, are not as important to larger cod as they are to cod during the early juvenile stage. A common pattern seen in ram-suction feeding carnivores like Murray cod is an ontogenetic shift from feeding on insects and small crustaceans during early juvenile stages, through to piscivory and feeding on larger crustaceans during late juvenile and adult stages (Amundsen *et al.* 2003; Stoffels 2013; Wainwright & Richard 1995; Winemiller 1989). Given this general shift in diet, growth of larger adult cod may only increase

during years that coincide with high rates of production of forage fishes and larger crustaceans. In river-floodplain systems, such years are usually characterised by a flood pulse of some magnitude, whereupon rewetting of habitats higher in the riverscape results in particularly strong pulses of energy through the food web (Balcombe & Arthington 2009; Bayley 1991; Benke 2001; McInerney *et al.* 2017; Winemiller 2004).

The ontogenetic pattern in the temperature dependence of Murray cod growth *in situ* may be a result of either (a) direct, size-based effects of physiology; or (b) the indirect effects of variation in the thermal response of different subsets of the riverine food web. There has been insufficient research on the thermal biology of riverine food webs to provide any convincing evidence for or against the second of these hypotheses. The pattern is, however, consistent with several studies of ontogenetic niche shifts in the fundamental thermal niche of fishes. That is, although we have no data on ontogenetic shifts in the thermal physiology of cod, other studies report a warming in preferred or optimal temperatures of thermal niche axes as fish age (Elliott & Elliott 2010; Hofmann & Fischer 2002; Schiemer *et al.* 2004).

Implications for management of riverine flows in a changing climate

The growth data we obtained from otoliths had an annual resolution, resulting in model predictions of mean growth rate over a year as a function of annual discharge and temperature. Given the 'per-year' units of our study, we are not in a strong position to inform the design of hydrographs within a year (sensu Acreman *et al.* 2014); hydrographs whose shape and magnitudes are defined in 'per-day' units of, say, ML d^{-1}. Instead, the research presented here has more relevance to management of annual water allocations and helping managers anticipate the risks to management objectives posed by climate change.

The results presented here add further weight to the case for maintaining and/or restoring long-term flow variability in riverine ecosystems (Bunn & Arthington 2002; Lytle & Poff 2004; Naiman *et al.* 2008). Given the ontogenetic variation in the discharge-growth relationship of Murray cod, we can infer that no single level of annual discharge leads to optimal growth of Murray cod. Interannual variation in annual discharge is required to optimise the growth of cod throughout their lifetime.

The discharge-growth curve for early juveniles indicates that years of median annual discharge result in optimal juvenile growth. This result demonstrates that the growth of juvenile cod can likely be optimised using in-channel environmental flows. This is an encouraging result given current water policy in the Basin constrains environmental flow delivery to in-channel flows (MDBA 2013).

With respect to late juvenile and adult Murray cod, the model indicates a linear increase in growth with annual discharge. It is possible this indicates a continuum of positive effects on food web processes, hence growth of cod, as annual discharge increases. By extension, it is tempting to infer that any increase in annual discharge caused by environmental water may promote various food web processes that enhance growth of Murray cod. However, we urge caution in drawing this inference as (a) there are a very large number of different per-day hydrographs for any level of annual discharge; and (b) our understanding of how river food web processes respond to in-channel flow variability is very poor. We recommend testing the hypothesis that food web productivity increases as a simple linear function of annual discharge in rivers. That is, there is a need to increase our understanding of the response of food web processes to flow variation at multiple temporal scales, so that we are better able to interpret the management significance of studies such as ours.

Following the IPCC, air temperature records up to 2006 are often used as a 'baseline' for evaluating climate change (IPCC 2013). Analysis of annual temperatures from our study systems during the baseline period showed that the mean annual temperature was 23.6 °C. This temperature coincided with peak growth of early juvenile cod. Indeed, the growth rate of early juveniles declined significantly with warming above the baseline annual temperature. Mean air temperatures are forecast to increase by as much as 5.3 °C by 2090 (CSIRO and Bureau of Meteorology 2015). Given

the forecast rate of warming, we may expect depressed growth of juvenile Murray cod under climate change forecasts for the Basin. Given growth may be related to recruitment, this magnitude of warming may lead to reduced recruitment of Murray cod.

By contrast the data indicate that the warming forecast for the Basin may promote growth of adult Murray cod. Consequently, there is much uncertainty around the overall effect of warming scenarios on Murray cod populations in the Basin.

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Appendix

Otolith collection and measurements

Otoliths from Murray cod and golden perch were obtained from six regulated river systems within the Murray-Darling Basin: The Gwydir, Lachlan, Murrumbidgee, Edward-Wakool, Goulburn and Lower Murray systems. Collections were made from a river segment ca. 100-400 km in length within each river system. These otoliths were from collections managed as part of a variety of projects, including the Australian Commonwealth Environmental Water Office's Long-Term Intervention Monitoring (LTIM) Project. Sagittal otolith sections were mounted on slides prior to being sent to the Murray-Darling Freshwater Research Centre where they were analysed.

Sagittal otolith sections were photographed using a Zeiss Axiocam ICc 5 camera mounted on a Leica MZ12.5 stereomicroscope with Zen 2.3 Blue Edition (Carl Zeiss Microscopy GmbH, 2011) microscopy software. Photographs were taken at x16 magnification for the measurement of annual growth increments, each of which consists of a translucent and an opaque band (Figure A 1). Broader translucent bands correspond to periods of higher growth during warmer months (i.e. spring and summer), followed by narrower opaque bands that correspond to lower growth periods during cooler months (i.e. winter and autumn). Photographs were taken at the highest possible magnification that allowed for the entire otolith section to be captured for the measurement of radii along the following axes: dorsal, proximal (dorsal-side), proximal (ventral-side), and ventral (i.e. x8 - 32 magnification depending on otolith section size).
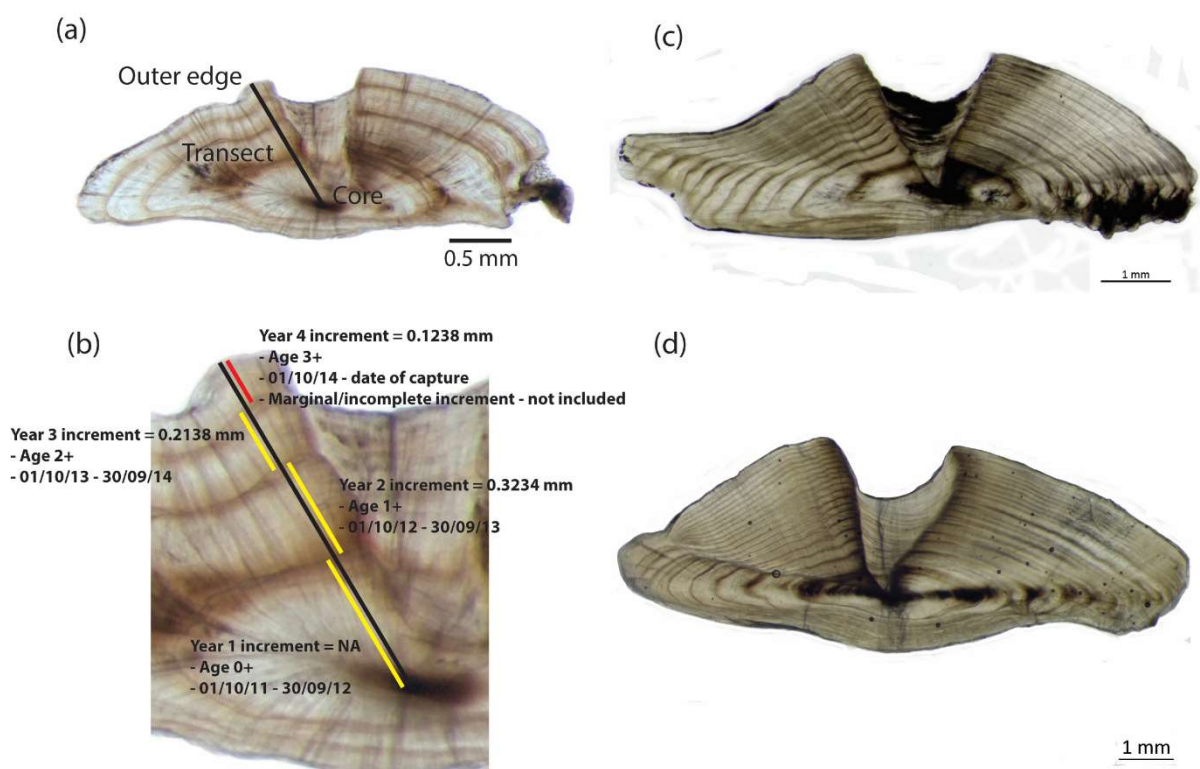
Figure A 1. Photographs illustrating otolith components (a) and how measurements were taken (b). Saggital otolith from a 12+ cod (c) and a 19+ golden perch (d).Otolith growth occurs at the outer edge, so the centre of the core (origin) is equal to age 0 and the outer edge corresponds with the capture date (Figure A 1). Fish were assigned a nominal birthdate of October 1st and annual growth increments were assigned 'growth year' t, such that Year t is from is 01/10/t to 30/09/t+1. Date of capture was known for every individual, enabling us to assign growth years and ages to each

increment (Figure A 1). Growth histories were created for each fish by measuring annual growth increments perpendicular to the axis of growth along a transect line that was established on the proximal axis, drawn from the core to the outer edge (following Morrongiello *et al.* 2011).

Results – further summaries of the otolith database

Table A 1 summarises the otolith increment data for this study.

Table A 1. Summaries of the otolith database. 'N sample years' refers to the number of years when fish were collected from rivers.

Catchment	N sample years	N fish	N increments	Age range (y)	Growth-year range	Biochronology length (y)
Murray cod, *Maccullochella peelii*						
Edward-Wakool	5	422	1920	1-28	1981-2014	34
Goulburn	3	45	152	1-9	2006-2014	9
Gwydir	1	87	432	1-18	1993-2011	19
Lachlan	1	38	218	1-9	2005-2013	9
Murrumbidgee	7	369	1402	1-22	1989-2013	25
Total Ns		*961*	*4124*			
Golden perch, *Macquaria ambigua*						
Edward-Wakool	4	144	571	1-16	1995-2014	20
Goulburn	3	57	352	1-20	1994-2014	21
Gwydir	1	51	222	1-18	1996-2013	18
Lachlan	1	53	178	1-17	1997-2013	17
Lower-Murray	1	72	396	1-17	1998-2013	16
Murrumbidgee	4	59	238	1-14	2001-2013	13
Total Ns		*436*	*1957*			

Figure A 2 and Figure A 3 present visual summaries of the Murray cod and golden perch otolith raw data, respectively. In addition to the information presented in the Results section of the report, certain features are worth noting:

A. Growth—as measured by increment width—is most variable for individual Murray cod and golden perch younger than 4+ (juveniles), particularly for 1+ individuals;

B. The vast majority of increment width data covers the 15-year period from 2000-2015;

C. Murray cod growth rate clearly varies among river systems (Figure A 2c) and—although to a smaller degree—golden perch (Figure A 3c). For instance, growth of Murray cod within Goulburn River is significantly lower than that observed in other systems. As another example, growth of 1+ and 2+ golden perch is particularly low within the Lower Murray River.

D. Otolith radius increases with fish length in both species. In golden perch, however, otolith radius continues to increase after fish length has reached an asymptote. As golden perch age, their depth:length ratio increases, much more so than for Murray

cod. Thus, increment width likely captures growth, when length does not. Increment width is a good proxy for growth in these species.

Figure A 2. Visualisation of the Murray cod otolith data. (a) Boxplots of the distribution of increment widths as a function of age. Thick horizontal lines are medians; the box is defined by the 25th and 75th percentiles (lower and upper quartile, respectively); dashed lines have lengths of 1.5 times the spread (spread = difference between quartiles). Points outside this range are outliers. (b) Visualisation of the chronology lengths of individual fish within the five catchments. (c) Mean increment width (± SE) as a function of age and catchment (colour coding same as in (b)). (d) Fish length as a function of otolith radius. Points indicate age of individual.
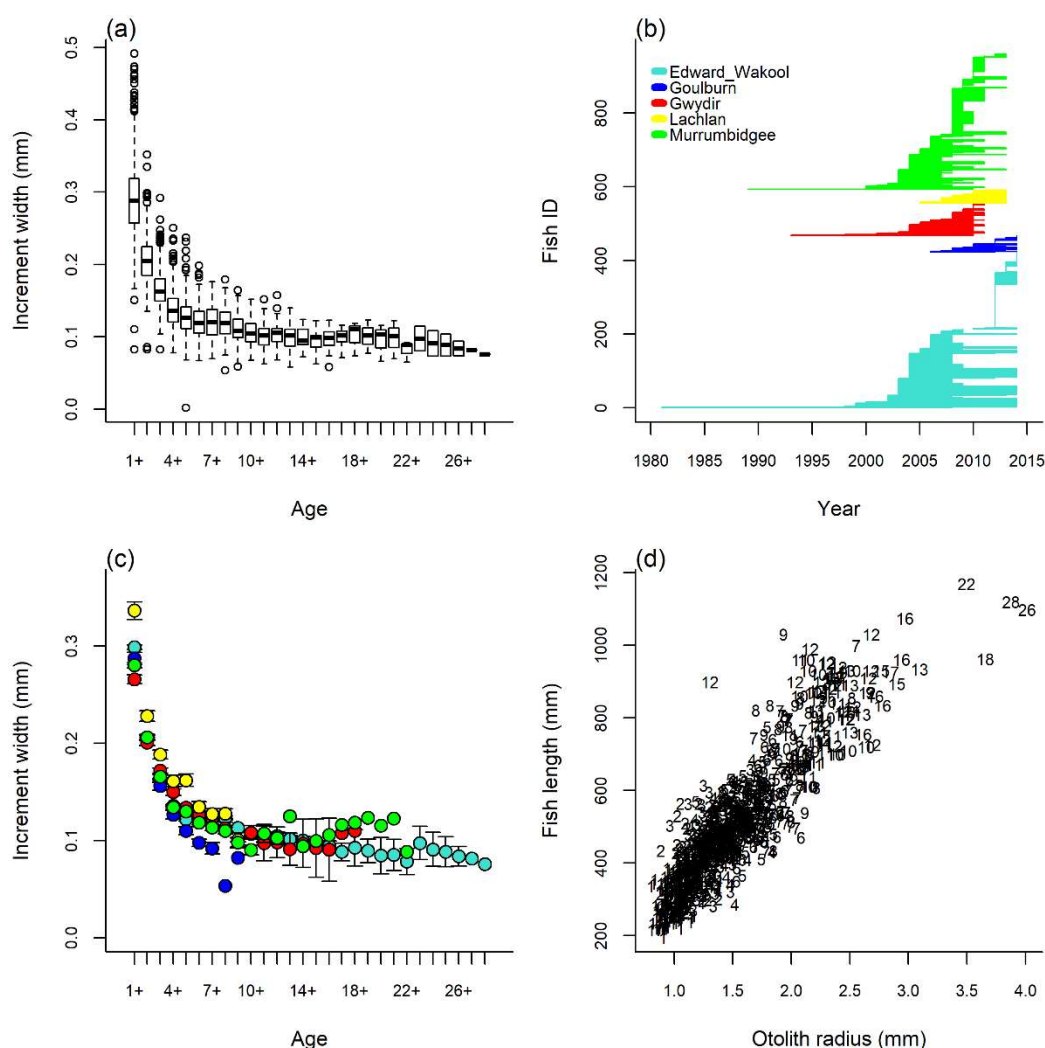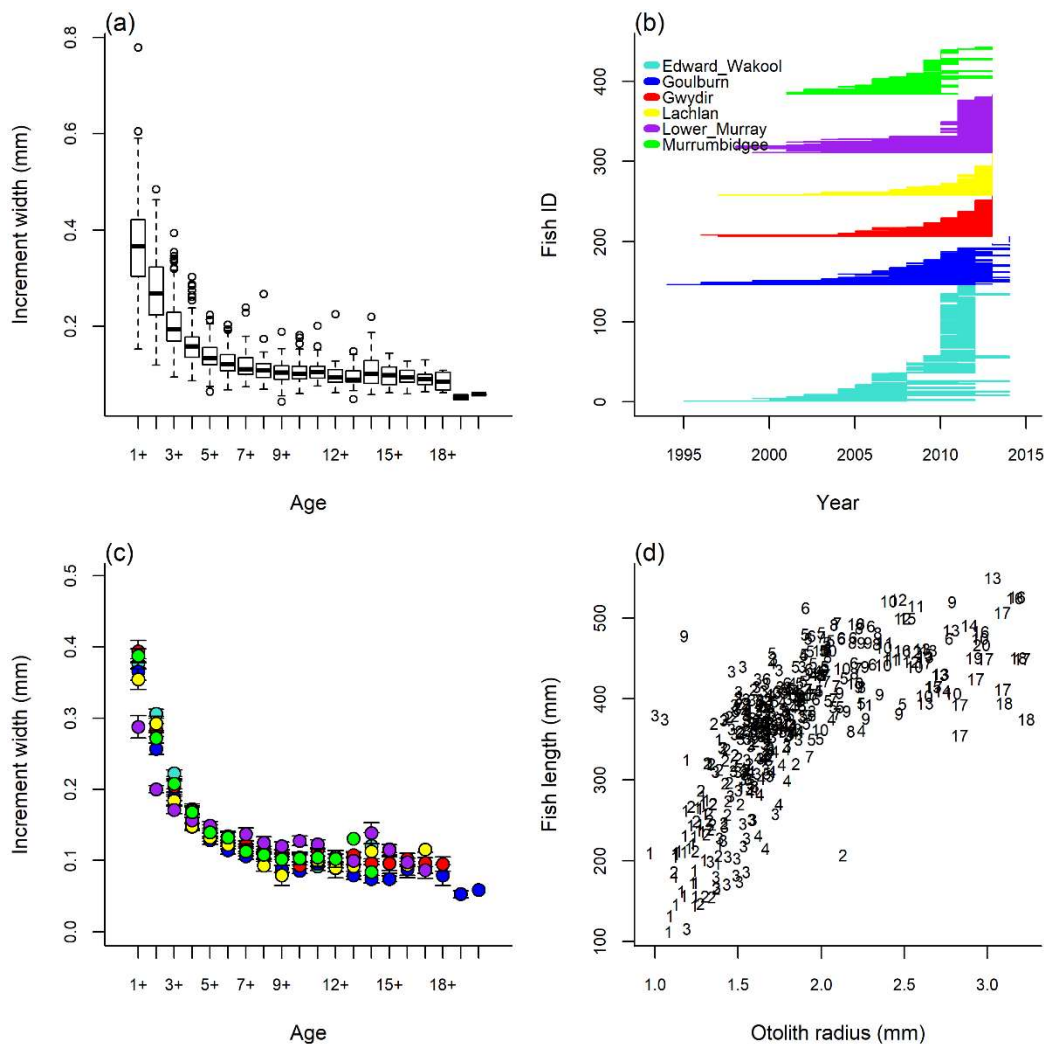
Figure A 3. Visualisation of the golden perch otolith data. (a) Boxplots of the distribution of increment widths as a function of age. Thick horizontal lines are medians; the box is defined by the 25th and 75th percentiles (lower and upper quartile, respectively); dashed lines have lengths of 1.5 times the spread (spread = difference between quartiles). Points outside this range are outliers. (b) Visualisation of the chronology lengths of individual fish within the five catchments. (c) Mean increment width (± SE) as a function of age and catchment (colour coding same as in (b)). (d) Fish length as a function of otolith radius. Points indicate age of individual.

River discharge and temperature gauge data

Daily discharge (ML d^{-1}) data were obtained from 18 gauges (Table A 2). Most river discharge gauges had logged over 35 years of daily discharge data. Air temperature was used as a surrogate for water temperature due to the paucity of water temperature logging stations throughout the Basin (Table A 2). Daily maximum and minimum air temperatures were sourced from the Australian Bureau of Meteorology (BOM). Air temperatures were paired with a discharge gauge by selecting the closest BOM station to the discharge gauge. For all BOM stations utilised, air temperature has been logged since prior to 1950, and so air temperature series had greater temporal coverage than those of river discharges.

Table A 2. River flow and air temperature gauges from which data were sourced for this study.

River system	Gauge name	Gauge Number	Mean discharge (ML/d)	Discharge SD	No. days	First year of discharge logging	BOM station name	BOM station No.
Goulburn	Murchison	405200	3227.3	7681.6	23421	1951	Tatura Sustainable Ag	81049
	McCoy's	405232	3792.9	7968.7	18831	1965	Kyabram	80091
Edward-Wakool	Wakool Offtake	409019	203.7	644.6	15559	1974	Deniliquin visitor centre	74128
	Yallakool Offtake	409020	400.3	934.1	22908	1954		
	Edward River, d/s Stevens	409023	2050.4	2638.5	15405	1973		
	Colligen Ck	409024	271.0	566.1	15542	1973		
Murrumbidgee	Narrandera	410005	8634.7	10512.9	16012	1973	Narrandera	74148
	Carrathool	410078	3617.9	5868.2	7783	1995	Hay Miller St	75031
Lachlan	Booligal	412005	742.5	1155.3	24032	1951	Hillston Airport	75032
	Hillston	412039	1136.2	1813.0	22502	1955		
	Whealbah	412078	622.6	1225.3	9273	1968		
Gwydir	Pallamallawa	418001	1804.3	5781.1	16259	1972	Moree Comparison	53048
Lower Murray	Lock 6	4260511	5994.7	6682.4	7189	1994	Renmark	24016
	Lock 5	4260513	8854.6	9016.6	10265	1981		
	Lock 4	4260515	7596.0	7059.5	6772	1994	Loxton Research Centre	24023
	Lock 3	4260517	7693.0	7943.8	7043	1994		
	Lock 2	4260519	7230.3	7230.9	7056	1994		
	Lock 1	4260903	16210.1	23365.6	18953	1951	Eudunda	24511

We did not have information about the movement history of individuals within river systems, so we made no attempt to pair individual otoliths with individual gauges at a fine spatial resolution. Instead, for each of the six river systems we generated a daily discharge time series that applies to each system as a whole. As such, any inference concerning the effects of discharge on growth pertains to mean flows moving through the system as a whole, not individual reaches or anabranches.

To obtain system-level mean daily discharges for the Goulburn, Murrumbidgee, Lower Murray and Lachlan, mean discharge for each day was determined across the gauges within each system (n ranges from two to four gauges for these systems; Table A 2). Mean daily discharge determined across gauges was appropriate for these systems as all gauges were on different reaches of the same single channel from which otoliths were sampled. By contrast, the Edward-Wakool and Gwydir systems comprise numerous braided channels, and the individuals from which otoliths were obtained may have moved through several of those channels throughout their lifetime. For these two systems we sought time series of the total mean discharge moving through the system per day. For the Gwydir, this series was easily obtained by using the Pallamallawa Gauge, situated just upstream of where the Gwydir bifurcates into the separate channels from which otoliths were obtained. To obtain mean daily discharge moving through the Edward-Wakool system, we summed daily discharge rates across four gauges situated on the four dominant distributaries of the Edward-Wakool (Table A 2).

Mean annual discharge was significantly positively correlated amongst gauges within river systems, as shown in Table A 3.

Table A 3. Mean, minimum and maximum pairwise correlation values for mean annual discharges within river systems.

River system	Mean correlation	Max. correlation	Min. correlation
Goulburn	0.87	0.87	0.87
Edward-Wakool	0.77	0.99	0.60
Murrumbidgee	0.82	0.94	0.66
Lachlan	0.63	0.98	0.44

Possible covariates of growth and screening their inclusion

Six variables were selected as possible environmental covariates with otolith increment width (mm), an index of fish growth (Table A 4).

Table A 4. Description of environmental covariates of otolith increment width used in the present analysis.

Covariate	Name in dataframes	Name in this report	Units
Mean annual standardised discharge, the mean of daily log-normal deviates for growth year t, where t is defined as $1/10/t – 30/9/t+1$.	Flow_logND_ave	F_t	Standard deviations of the log-normal random variable
Difference in mean annual standardised discharge, in growth year t, relative to year t-1: $\Delta F_t = F_t - F_{t-1}$, such that when $\Delta F_t < 0$ standardised discharge is decreasing; when $\Delta F_t = 0$ standardised discharge is stable; when $\Delta F_t > 0$ standardised discharge is increasing.	Flow_DeltaMean	ΔF_t	Standard deviations of the log-normal random variable
The number of very low-flow days last year. A 'very low flow day' was a day where the standardised discharge was less than or equal to the 10th percentile of the distribution of log-normal deviates for that river system.	vLowDaysLY	nLF_{t-1}	Number of days
The number of warm days. The number of days during growth year t where maximum air temperature was $\geq$ 25°C and $<$ 35°C. Essentially the number of days when conditions should be favourable for growth.	warmGrowthdays	nWT_t	Number of days
The number of hot days. The number of days during growth year t where maximum air temperature was $\geq$ 35°C. Taken as an index of magnitude of heat stress during a growth year, when growth may be suppressed.	hotGrowthDays	nHT_t	Number of days
Mean maximum daily air temperature for growth year t.	maxAirTemp_ave	T_t	Degrees Celsius

Mean annual standardised discharge ('annual discharge', F_t) should be positively related to the volume of foraging habitat available to Murray cod. Further, this positive relationship is likely nonlinear, such that beyond some threshold of annual discharge, the surface area of river-floodplain habitat inundated increases exponentially, as flows spill out onto anabranches, benches and other floodplain habitats (Benke 2001).

The *difference in mean annual standardised discharge* (ΔF_t) may affect growth in addition to annual discharge. Consider an annual discharge rate of $F_t = x$ during the growth year t. If annual discharge during the previous year was lower ($F_{t-1} < x$) then annual discharge has increased ($\Delta F_t > 0$) and inundation of allochthonous material may result in a 'boom' of secondary production on the floodplain (McInerney *et al.* 2017), which may in turn result in particularly high growth for that level of $F_t = x$. At that same level of discharge, $F_t = x$, a lower growth rate may result when annual discharge is declining compared to the previous year ($\Delta F_t < 0$), given a lower rate of sequestration of allochthonous material into the aquatic food web. Thus, both annual discharge and change in annual discharge may be important drivers of growth.

Fish often exhibit particularly high rates of growth following periods of physiological stress and/or low energy consumption (Ali *et al.* 2003). It follows that, for any specified annual discharge level, growth may be higher at that level of annual discharge if it follows a year of particularly low flows, when food may have been scarce. The *number of very low flow days in the previous year* (nLF_{t-1}) was considered to account for any compensatory growth effects.
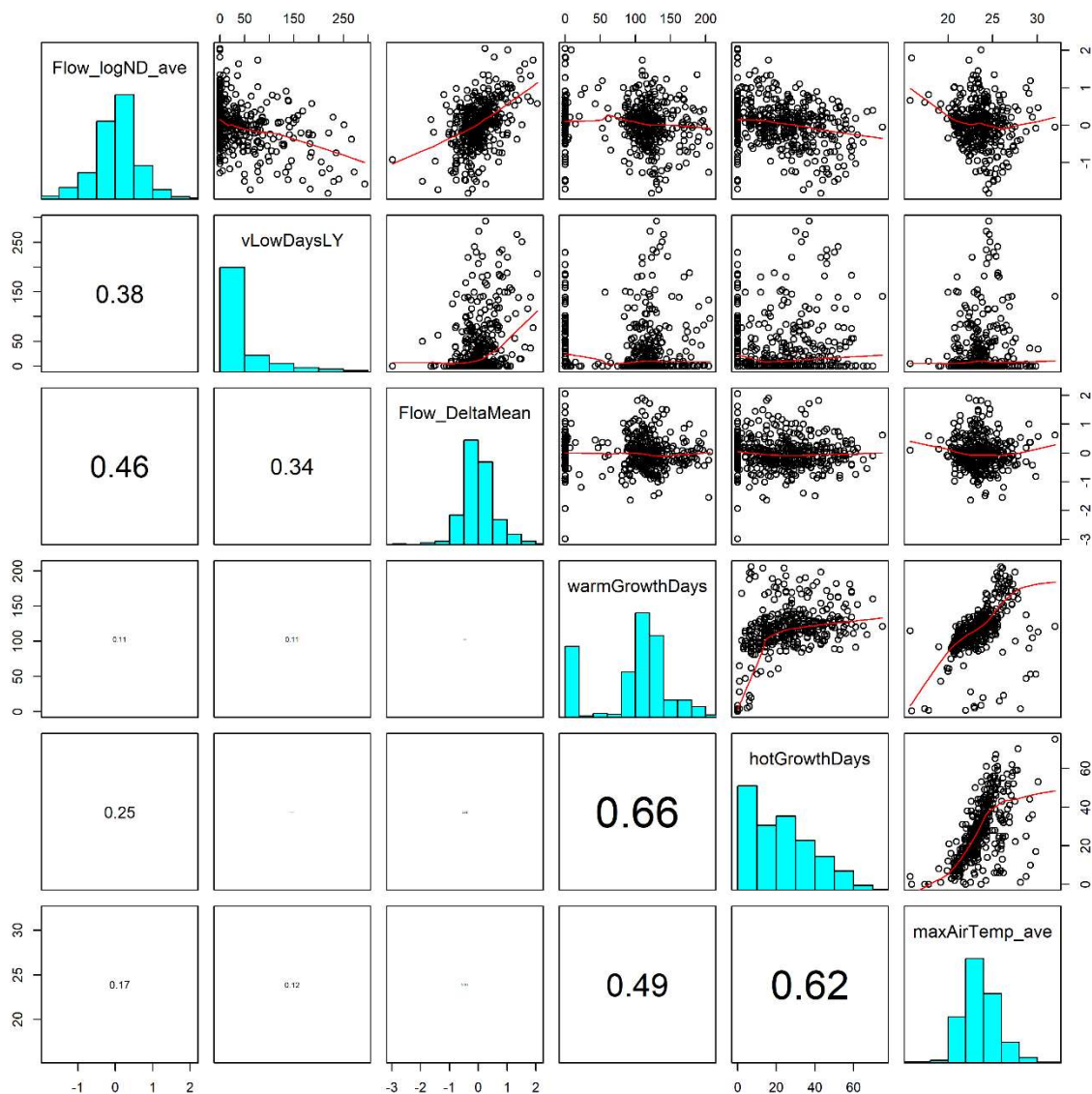

Figure A 4. Matrix plot describing the distributions of, and correlations among, the possible environmental covariates. Diagonal elements show frequency distributions of covariate values. Lower diagonal matrix presents Pearson correlation coefficients. Upper diagonal matrix presents

scatterplots among covariates, including loess smooths. Refer to Table A 4 for variable descriptions.Being ectotherms, temperature has a very strong influence on fish growth (Jobling 1996). Two alternative parameterisations of temperature effects were considered: The first approach considered was based on the number of days within a growth year when temperature was favourable (*the number of warm days* (nWT_t); positive relationship with growth hypothesised; Table A 4) or too hot (*the number of hot days* (nHT_t); negative relationship with growth hypothesized (Table A 4). This approach was considered with a view to decomposing temperature effects into two linear covariates—one positively and one negatively related to growth—such that temperature effects might be included as parametric ('non-smoother') terms in the generalised additive mixed models (GAMMs). The alternative approach was to simply model temperature effects as a curvilinear (non-parametric, smoothed) term in the GAMMs.

High collinearity among model covariates can lead to spurious inferences and predictions (Wood 2017; Zuur *et al.* 2009). Figure A 4 presents a graphical overview of the distributions of, and collinearity among, the six environmental covariates. It was evident that the two approaches for modelling temperature effects were mutually exclusive as maxAirTemp_ave is closely positively correlated with both the number of warmGrowthDays and hotGrowthDays. Against a parameterisation based on the number of warm and hot days was the fact that the number of hotGrowthDays was negatively correlated with mean annual standardised discharge (Flow_logND_ave; Figure A 4). By contrast, maxAirTemp_ave was not correlated with any flow variable (Figure A 4). Accordingly, mean maximum daily air temperature of a growth year was the variable selected to account for temperature effects on growth, to be included in GAMMs—at least in the first instance—as a smoothed term.

Pearson correlation coefficients indicated relatively weak, but potentially problematic correlations between Flow_logND_ave, vLowDaysLY and Flow_DeltaMean (Figure A 4). We wished to avoid spurious inferences, so the only flow variable included in the candidate model set was annual discharge (Flow_logND_ave).

Analysis of final Murray cod model – covariate effects and uncertainty around those effects

We used simulation to analyse the effect of either annual discharge or temperature on Murray cod growth at key ages, and how much uncertainty around that effect is generated by (a) environmental uncertainty, and (b) both environmental uncertainty and uncertainty in model parameter values (statistical uncertainty). In a decision-making context, environmental uncertainty arises when the ecological outcomes from varying one variable may be affected by variation in other environmental variables with which our focal variable interacts. Our use of the expressions environmental and statistical uncertainty follows the nomenclature of Conroy and Peterson (2013). In this analysis of uncertainty, we also include the random effect of river, to better understand how consistent growth responses—and the associated uncertainties—were across rivers.

The output of this analysis was a set of boxplots for each extrinsic, fixed covariate: annual discharge and temperature. For each of five rivers and three ages (see below) we generated two (forms of uncertainty) × p (levels of the fixed, extrinsic covariate) = $2p$ boxplots.

For annual discharge we determined the distributions of predicted growth rates for p = 7 levels, hence 2 × 7 = 14 boxplots per river-age pairing. These seven levels of annual discharge were defined by the following percentiles of the domain of annual discharge values in the training data set: 5; 10; 25; 50; 75; 90; 95%.

For annual temperature we determined the distributions of predicted growth rates for p = 6 levels, hence 2 × 6 = 12 boxplots per river-age pairing. These six levels of annual temperature were defined

by the integer sequence 22, 23,…,27 °C. The first and last value of this sequence (22 °C and 27 °C) were approximately the 10th and 90th percentiles, respectively, of the temperature data in the training set.

Differences in the growth response to annual discharge and temperature were observed among early juveniles (1+ to 2+), late juveniles (3+ to 5+) and adults (see Results). Therefore, this model analysis focused on three age-classes representative of these three stages: 1+, 5+ and 11+.

Each individual boxplot was comprised of 30 predictions of annual growth, generated by using the final GAMM over a 34-year annual discharge or temperature series—the observed series for each river from 1981-2014. The algorithm for analysing effects of annual discharge was as follows:

4. Within each of the five rivers, obtain the 34-year annual temperature series of that river.

5. For analysis of effects incorporating environmental uncertainty alone, predict annual growth across the 30-year annual temperature series for each value of age (1+, 5+ or 11+), crossed with each value of annual discharge for that river (5; 10; 25; 50; 75; 90; 95%). These predictions of annual growth include the fixed, population-wide effect plus the random, river-specific effect, and any temporal autocorrelation.

6. For prediction of effects incorporating both environmental and statistical uncertainty, Step 2 is followed but now each population-wide (fixed) estimate of annual growth is obtained by drawing from a random-normal distribution with a mean defined by the fixed growth estimate, and standard deviation defined by the prediction error of the GAMM. Prediction errors are easily extracted from the gamm objects returned by the mgcv R package, and are assumed to be normally-distributed (Wood 2017). This fixed annual growth estimate—with prediction error—is then added to the deviation induced by the river random effect.

7. Repeat for the remaining four rivers.

The algorithm for analysing effects of annual temperature followed that outlined above, but where predictions were made across a 30-year discharge series with the aforementioned fixed values of temperature.

Additional examination of the final GAMM

It is evident from **Figure A 5** that the final model of Murray cod growth fits the data very well. No substantial heteroscedasticity is evident from the residuals and significant bias is rare.
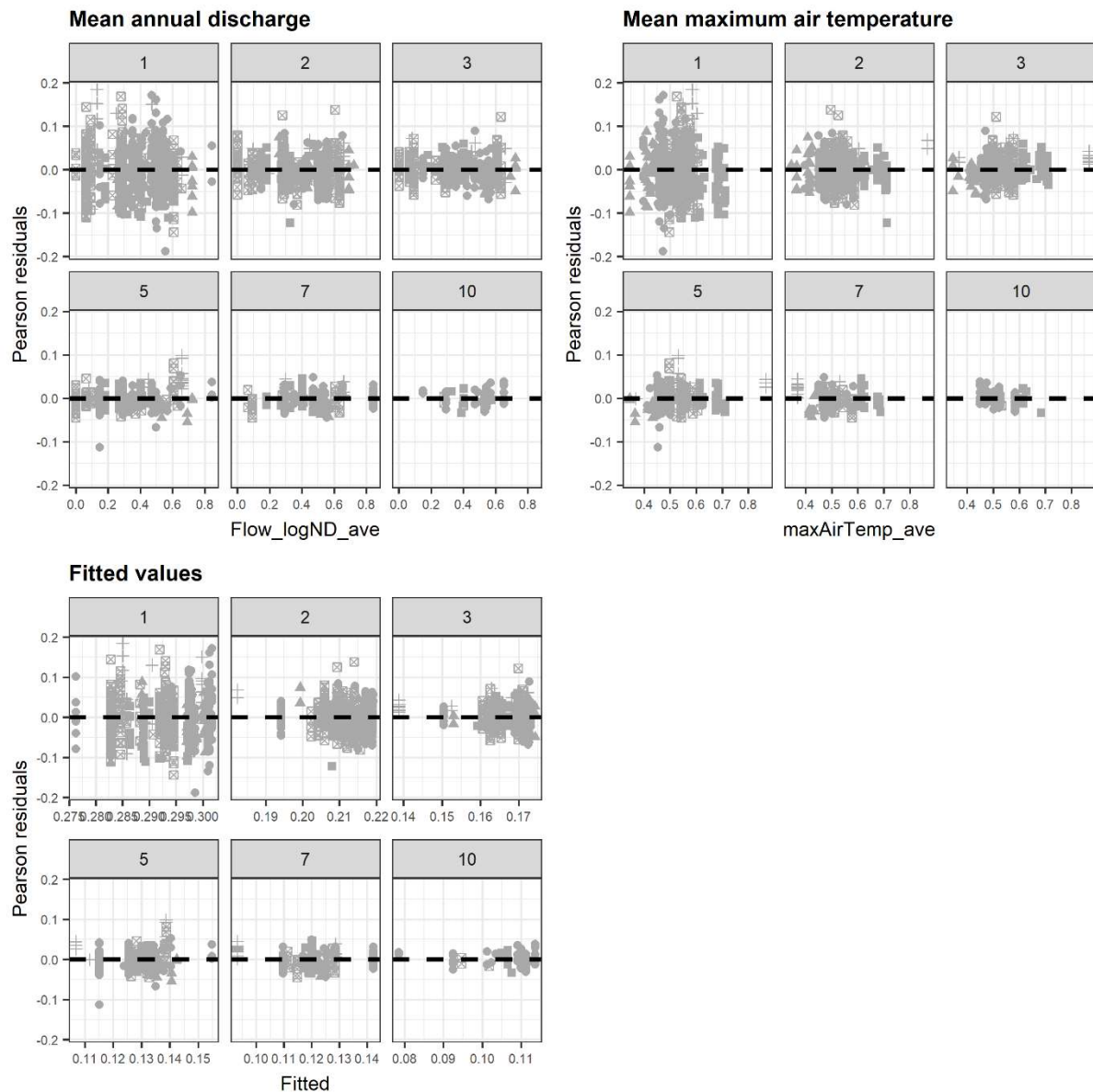
Figure A 5. Pearson residuals of the best Murray cod growth model as a function of the covariates and predicted values. Figure A 6 presents the fixed-effects model fits of the final GAMM, showing age-specific responses of Murray cod growth to annual discharge and temperature. Differences in response among age were most noticeable between early juvenile (ca. 1+ to 2+), late juvenile (ca. 3+ to 5+) and adult (> 5+) stages. Accordingly, the Results and Discussion present plots representative of these three stages only, to save space and for ease of interpretation.
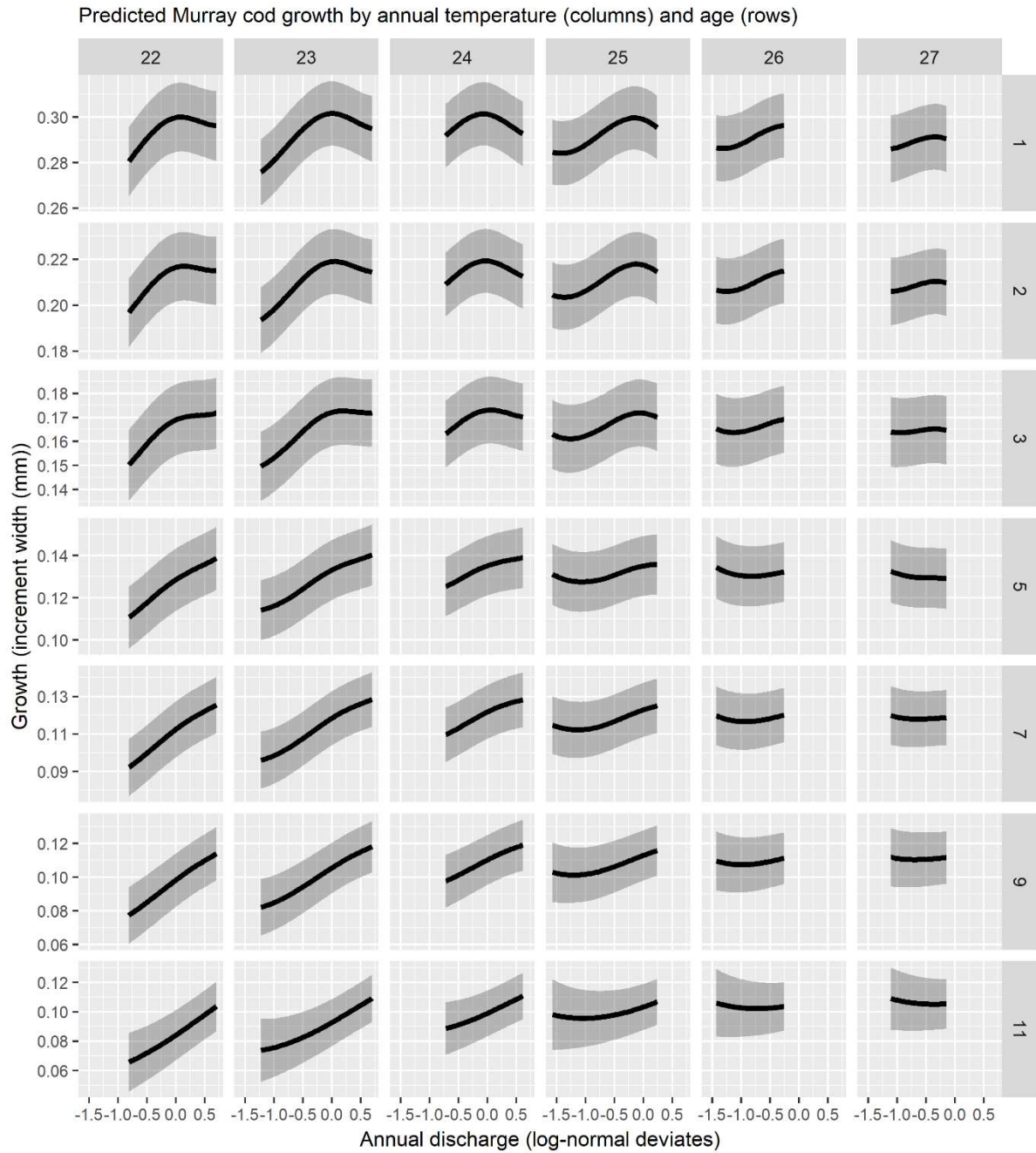
Figure A 6. Fitted model (± 95% CI) of Murray cod growth as a function of annual discharge at six annual temperatures (22 – 27 °C) and seven ages (1, 2,...11). Model fits are not extended beyond the domain of annual discharge data within each annual temperature level (domain within each temperature level, x, defined as [x-0.5, x+0.5]).