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Stage-dependent effects of river flow and temperature regimes on the growth dynamics of an apex predator

Running title: Climate and river flow drive fish growth

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Abstract

In the World's rivers, alteration of flow is a major driver of biodiversity decline. Global warming is now affecting the thermal and hydrological regimes of rivers, compounding the threat and complicating conservation planning. To inform management under a non-stationary climate we must improve our understanding of how flow and thermal regimes interact to affect the population dynamics of riverine biota. We used long-term growth biochronologies, spanning 34 years and 400,000 km², to model the growth dynamics of a long-lived, apex predator (Murray cod) as a function of factors extrinsic (river discharge; air temperature; sub-catchment) and intrinsic (age; individual) to the population. Annual growth of Murray cod showed significant, curvilinear, life-stage-specific responses to an interaction between annual discharge and temperature. Growth of early juveniles (age 1+ and 2+ years) exhibited a unimodal relationship with annual discharge, peaking near median annual discharge. Growth of late juveniles (3+ to 5+) and adults (> 5+) increased with annual discharge, with the rate of increase being particularly high in adults, whose growth peaked during years with flooding. Years with very low annual discharge, as experienced during drought and under high abstraction, suppress growth rates of all Murray cod life-stages. Unimodal relationships between growth and annual temperature were evident across all life-stages. Contrary to expectations of the Temperature Size Rule, the annual air temperature at which maximum growth occurred increased with age. The stage-specific response of Murray cod to annual discharge indicates that no single magnitude of annual discharge is optimal for cod populations, adding further weight to the case for maintaining and/or restoring flow variability in riverine ecosystems. With respect to climate change impacts, on balance our results indicate that the primary mechanism by which climate change threatens Murray cod growth is through alteration of river flows, not through warming annual mean temperatures *per se*.

Keywords: discharge; climate change; fish; flow; growth; recruitment; river; Temperature Size Rule; thermal niche

65

66 1. INTRODUCTION

67 Freshwater biodiversity is declining at an alarming rate (Vorosmarty et al., 2010). One of the
68 dominant drivers of this decline is alteration of natural riverine flow regimes (Best, 2019).
69 Although considerable progress has been made in understanding how alteration of flow
70 regimes affects biodiversity, major scientific challenges are ahead of us (Poff, 2018; Stoffels,
71 Bond, & Nicol, 2018). One such challenge comes from climate change imposing a form of
72 non-stationarity on riverine flows management (J. D. Tonkin et al., 2019). That is,
73 contemporary flow-ecology relationships, and the decision problems formulated today, may
74 be altered by climatic change (Stoffels et al., 2018). For example, climate change is
75 compounding the effects of river regulation by altering the thermal regimes of rivers
76 (Seneviratne, Donat, Mueller, & Alexander, 2014; van Vliet, Ludwig, & Kabat, 2013; Wu et
77 al., 2012). Environmental temperature is one of the most important drivers of population
78 processes in ectotherms (Kingsolver & Huey, 2008). The traits of riverine species have
79 evolved in response to the natural flow regime (Lytle & Poff, 2004), but they have also
80 evolved in response to the natural thermal regime (Humphries et al., 2020; Olden & Naiman,
81 2010). To better inform the management of riverine species, most of which are ectotherms,
82 we require an improved understanding of how those species respond to interactions between
83 flow and temperature.

84

85 Animals with indeterminate growth, such as fish, generally exhibit responses to
86 environmental change that are dependent on life-stage. These stage-specific responses play a
87 fundamental role in shaping the dynamics of populations and communities in response to
88 environmental change (Audzijonyte, Kuparinen, Gorton, & Fulton, 2013; de Roos & Persson,
89 2013; Lindmark, Huss, Ohlberger, & Gårdmark, 2018; Werner & Gilliam, 1984). Growth rate
90 determines the speed with which individuals transition through ontogenetic stages and so, in
91 turn, influences the rates of other processes like stage-specific mortality (Policansky, 2015;
92 Tanaka, Satoh, Iwahashi, & Yamada, 2006; Vincenzi, Satterthwaite, & Mangel, 2012). For
93 example, varying river flows have been found to have greatest impact on growth of juvenile
94 fishes (Davidson, Letcher, & Nislow, 2010; Nislow, Sepulveda, & Folt, 2004; Nunn, Harvey,
95 Britton, Frear, & Cowx, 2007; Spurgeon & Pegg, 2017). Nonetheless, very few studies report
96 stage-specific growth dynamics of riverine fishes using data that (a) spans all or most of the
97 ages in the population, and (b) comprise growth time series of multiple ages exposed to the

same long-term hydrological series (but see Morrongiello, Walsh, Gray, Stocks, & Crook, 2014; Z. Tonkin et al., 2017). With respect to temperature, we know that the thermal performance curves of an ectotherm may vary through ontogeny (Peck, Clark, Morley, Massey, & Rossetti, 2009), yet our understanding of the direction and magnitude of that variation is surprisingly poor for all ectotherms (Ohlberger, 2013; Sinclair et al., 2016). Laboratory experiments generally indicate that juveniles ($\geq 1+$ age) of fishes with medium-high longevity tend to have ‘warm-shifted’ thermal performance curves relative to adults, perhaps conferring juveniles greater resilience to warming than adults (Clark et al., 2013; Messmer et al., 2017; Peck et al., 2009; Peck, Souster, & Clark, 2013). Surprisingly, however, our knowledge of how temperature interacts with ontogenetic stage to affect growth curves of fishes with medium-high longevity is poor, even for species of high socioeconomic importance that have been extensively studied (e.g. Jonsson & Jonsson, 2009). Faster juvenile growth and maturation, coupled with retardation of adult growth under warming is a pattern expected under the Temperature Size Rule (TSR; Atkinson, 1994; Audzijonyte et al., 2019). Empirical tests of the TSR have mostly come in the form of documented shifts in population size composition towards smaller individuals as habitat temperature warms (Baudron, Needle, Rijnsdorp, & Tara Marshall, 2014; Daufresne, Lengfellner, & Sommer, 2009; Horne, Hirst, & Atkinson, 2017; van Rijn, Buba, DeLong, Kiflawi, & Belmaker, 2017). Although such compositional shifts are an emergent result of the mechanisms proposed under TSR, other non-thermal causes may produce the same shifts, and so there is a need for studies of the concurrent, stage-specific growth dynamics of ectotherms, to test the applicability of the TSR to wild populations (Audzijonyte et al., 2019; Lindmark et al., 2018; Ohlberger, 2013).

Here we used a novel data set spanning 34 years and multiple sub-catchments covering ca. 400,000 km² across Australia’s Murray-Darling Basin (MDB) to improve our understanding of how the growth dynamics of an iconic apex predator, Murray cod (*Maccullochella peelii*, Mitchell 1838; Percichthyidae), responds to interannual dynamics of flow and temperature. Long-lived apex predators are of global interest due to their top-down, often cascading, effects on multiple species in the food web (Estes et al., 2011; Ripple et al., 2014). There have also been recent calls for an improved understanding of the population dynamics of freshwater ‘megafauna’ species (freshwater animals that can reach a body mass ≥ 30 kg), which have traits conferring high susceptibility to the degradation of freshwater ecosystems, and are therefore of global conservation concern (He et al., 2019). The Murray cod has the physiological and life-history traits of a freshwater megafauna species (He et al., 2019), and

so knowledge of its response to flow and thermal regimes will facilitate improved management of freshwater megafauna. We partitioned a mix of ‘intrinsic’ and ‘extrinsic’ factors that may drive growth dynamics (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/stage 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 accounted for the effect of river system on the sub-populations studied. We expected the growth response of Murray cod to be a unimodal function of temperature (Kingsolver, 2009; Wootton, 2011), and that the growth curve of juveniles would be warm-shifted relative to adults, consistent with the TSR (Atkinson, 1994). The literature concerning the response of fish growth to river flows is not sufficiently well developed to offer meaningful stage-specific hypotheses. However, we generally anticipated a positive relationship between discharge and Murray cod growth, consistent with recent studies of other species and the Flood Pulse Concept (Izzo et al., 2016; Junk, Bayley, & Sparks, 1989; Z. D. Tonkin, King, Robertson, & Ramsey, 2011).

2 MATERIALS AND METHODS

2.1 Study species

The Murray cod is Australia’s largest freshwater fish reaching ca. 114 kg and 180 cm in length and is endemic to Australia’s MDB (Lintermans 2007). It is an iconic species, featuring strongly in Aboriginal Australian mythology and is one of Australia’s most valued freshwater sportfish (Lintermans, 2007). Large adults are apex carnivores in the food webs of the MDB (Ebner, 2006), and although capable of large-scale movement, generally have a well-defined home range restricted to a length of river < 1 km (Koehn et al., 2009; Koehn & Nicol, 2014; Leigh & Zampatti, 2013; Thiem et al., 2018).

2.2 Data collation

Full descriptions of data collation and measurements for (a) otoliths and (b) flow and temperature are provided in Appendices S1 and S2, respectively, and briefly summarised here.

Murray cod otoliths were obtained using various fishing methods from five regulated river systems: The Gwydir, Lachlan, Murrumbidgee, Edward-Wakool and Goulburn rivers.

Collections were made from a river segment ca. 100–400 km in length within each river system. Photographs of the sagittal section of each otolith 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, Crook, King, Ramsey, & Brown, 2011). Fish were assigned a nominal birthdate of October 1st (approximate hatch date of larval cod, on the average) and annual growth increments were assigned ‘growth year’ t (such that growth year t is 01/10/ t to 30/09/ $t+1$; note that much of the flow contributing to growth year t comes from calendar year $t+1$). Capture date was known for all individuals, enabling us to assign growth years and ages to each increment (Appendix S1).

Daily discharge (ML d^{-1}) data were obtained from 12 gauges within study segments (Table S2). Air temperature was used as a surrogate for water temperature due to the paucity of water temperature logging stations throughout the MDB (Table S2). Use of air temperature as a proxy for water temperature was valid for two reasons: First, in our case it was not essential to develop a model to infer or predict the effects of absolute water temperature. Second, river water temperature is an increasing function of air temperature, and air temperature explains the majority of variance in water temperature in rivers like the ones studied here, especially when temperature data has an annual resolution (Mohseni, Stefan, & Erickson, 1998; van Vliet, Ludwig, Zwolsman, Weedon, & Kabat, 2011; Webb, Clack, & Walling, 2003). Further justification is provided in Appendix S2. 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 rivers, so we made no attempt to pair individual otoliths with individual gauges at a fine spatial resolution. Instead, for each of the five rivers we generated a daily discharge time series that applies to each river as a whole. As such, any inference concerning the effects of discharge on growth pertains to mean flows moving through a river, not individual reaches or anabranches (Appendix S2). This approach was supported as pairwise correlations of the mean annual discharges between gauges within rivers were significantly positive (Table S3).

2.3 Model parameterisation, selection and testing

Prior to the calculation of any hydrological covariate, time series of mean daily discharge were transformed into standard, log-normal random deviates (Wackerly, Mendenhall, & Scheaffer, 2002). This allowed us to take discharge distributions from rivers with different means and standard deviations, and give them the same location (zero) and standard deviation (one). Discharge standardisation was carried out for each gauge prior to obtaining system-level annual (growth year) means.

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 simple 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. We examined the effects of two fixed covariates on growth: 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*’). Other hydrological and temperature covariates were considered but these were collinear and so were not included (Appendix S3). Annual discharge 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, increasing not only habitat but production of food resources (Benke, 2001; McInerney, Stoffels, Shackleton, & Davey, 2017). Being ectotherms, temperature also has a strong influence on fish growth, and hence was included in the models (Jobling, 1996).

Graphical examination of the relations between covariates and increment widths showed that curvilinear relations were common. These curvilinear 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; S. N. Wood, 2017) for modelling G as a function of covariates. The set of 10 candidate GAMMs is described in Table 1.

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 extrinsic impacts of river system and year on G ; (2) four models that added the extrinsic factors of primary interest in this paper—effects of annual discharge and temperature; (3) as for (2), but including temporal autocorrelation in G (Table 1). The last class of models was parameterised to account for temporal autocorrelation amongst residuals, as significant temporal autocorrelation can affect inferences if unaccounted for (Zuur, Ieno, Walker, Savaliev, & M., 2009). In addition, the presence of strong temporal correlation may indicate multi-year biological processes are influencing growth rates, but which are unaccounted for within the fixed components of models.

The candidate model set was mostly nested, such that simpler models were subsets of more complex models. The exception was Null 2, which included a crossed random factor to account for the effect of year on growth variability within rivers (Table 1). The year effect in Null 2 enabled us to include a factor that might account for all drivers of interannual variation in growth, not just those of discharge and temperature. As such, Null 2 makes for a useful comparison with Models E1-E8; if Null 2 has a high probability of being the most likely model in the candidate set, given the data, then that indicates factors other than flow and temperature may be having a significant influence on the interannual growth dynamics of cod.

Null 2 was not a subset of E1-E8 due to limitations of the various R packages used for GAMMs. Given our analysis is a time series analysis, accounting for possible temporal autocorrelation was considered a priority. The *mgcv* package enables inclusion of autocorrelation terms and was used for estimating the parameters of Null 1 and E1-E8 (S. N. Wood, 2017). However, the *mgcv* package does not easily accommodate crossed random factors so the *gamm4* package was used to fit Null 2 to the data (S. Wood & Scheipl, 2017). Generalised cross-validation was implemented to ensure individual smooth terms were not overfitted to data (S. N. Wood, 2017).

Selecting among competing mixed-effects models is an area of active statistical research and there is currently no consensus on which approach performs best (Bolker et al., 2009; Wang & Gelman, 2015). We used an information-theoretic approach for model selection (Burnham & Anderson, 2002), based on the Akaike Information Criterion (AIC; Akaike, 1974). We also trialled a k -fold cross-validation approach to model selection (Hastie, Tibshirani, & Friedman, 2009), but found it a less sensitive tool for mixed-effects model selection than AIC, following the more general observation of Wang and Gelman (2015). The objective of this analysis was to yield general inferences and predictions concerning how Murray cod growth responds to discharge and temperature. We therefore tested the predictive accuracy of the final GAMM using data independent to that used for parameter estimation. 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 $-\infty$ 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.

2.4 Analysis of final model and uncertainty

Age typically accounts for most of the variance in growth of long-lived fishes (Morrongiello & Thresher, 2015). To isolate and quantify the magnitudes of the combined effects of annual discharge and temperature, we estimated age-specific magnitude of covariate effects as the range of fitted values (fixed effects + random effect of river) within an age (R_f), expressed as a percentage of the range of raw increment widths within that age (R_o) (e.g. Izzo et al., 2016): $(R_f/R_o) \cdot 100$. We also determined the relative effect sizes of annual discharge and temperature on Murray cod growth. We used the final model to predict the range in growth of three life-stages (see Results) as a function of one covariate while fixing the value of the other at its median value, within each respective river. When estimating the effect size of a

covariate we predicted range of growth over a domain bound by the first and third quartiles, to ensure any outliers in the tails of the covariate distributions did not influence our estimates of effect size.

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. How will the main effects of annual discharge and temperature affect growth across yearly ages, and how much uncertainty in that relationship is generated by (a) the interaction one covariate has with the other among years; and (b) the interaction one covariate has with the other among years and uncertainty in the value of GAMM parameters?
2. How consistent are answers to the above two questions across river systems?

Two fixed, extrinsic covariates were the focus of this uncertainty analysis: annual discharge and annual temperature. At its core the algorithm for this uncertainty analysis 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. Appendix S4 explains this analysis in detail.

3. RESULTS

Our database comprised 4124 growth increments from 961 Murray cod otoliths. Biochronology lengths ranged from 9 to 34 years among rivers (spanning 1981 – 2014), with growth estimates from ages 1+ through to 28+ (Appendix S1).

Given the data and the set of candidate models, Model E8 (three-way interaction between age, standardised discharge and temperature + autocorrelation term) was by far the most likely model of Murray cod growth dynamics, with an Akaike weight of one. Relative to E8, all other models tested had very low probability of being the most likely model in the set

(Table 2). The four models that included temporal autocorrelation of growth were among the five most likely models in the candidate set. Null 1 was the least likely model in the candidate set, but Null 2 was the second most likely model (Table 2).

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 1). There was weak evidence for a significant effect of the third smooth term, the interaction between age and temperature ($F = 0.57$; $P = 0.72$), so that term was dropped from Model E8 to yield the final model, presented in Table 3 ($AIC = -13897$; $\log(L) = 6966$). This final model fit the data well, with generally homogeneous residuals and no bias evident in the fit (Appendix S5). Predictive accuracy, as measured using NSE, was 0.79, which was comparable with the variance explained in the training data by the model (Table 3).

One of the most notable features of the final model's random component was the high temporal autocorrelation among residuals through time. The estimated value of ρ was 0.49, meaning that, after we accounted for the variance explained by flow and temperature covariates, residual variation in Murray cod growth was significantly correlated among years (Table 3). Variation in random intercepts among individuals within rivers was low, but variation in random intercepts among rivers was approximately half that of residual error (Table 3). The intraclass correlation coefficient (Gelman & Hill, 2007) for growth among individuals within rivers was 0.18, while the correlation in increment widths within individuals, within rivers was also 0.18 (identical at two significant digits due to the very small value of σ_2). Growth rate declined with age (Table 3; Appendix S1) and the global R^2 of the model including only spatial and intrinsic effects of age and individual (Null 1) was 0.80. The R^2 of the final extrinsic model was 0.82 (Table 3).

Annual discharge and temperature had significant age-dependent effects on growth (Table 3; Appendix S5). The magnitude of the combined effects of annual discharge and temperature on Murray cod growth varied between ca. 16 and 56% of the total range of observed age-specific growth (including measurement error; Figure 1). These effect sizes increased with age until individuals reached an age of approximately 10+ (Figure 1). Differences in the

shape of the growth response to annual discharge and temperature were most salient among ‘early juvenile’ (ca. 1+ to 2+), ‘late juvenile’ (ca. 3+ to 5+) and ‘adult’ (> 5+) life stages (Appendix S5). For ease of interpretation, subsequent analysis, figures and discussion are presented in the context of these three life-stages. Predictions were based on a single representative age within each class: 1+ (early juvenile); 5+ (late juvenile); and 11+ (adult). The final model (Table 3) indicated annual discharge had a larger effect size than annual temperature. Annual discharge generally had a stronger effect on interannual variability in the growth rates of early juvenile, late juvenile and adult Murray cod than did annual temperature (Figure 2).

The temporal domain of our training data (1981–2014) encompassed two major floods and the Millennium Drought ca. 2000–2010 (van Dijk et al., 2013) (Figure 3). It included a warming trend across all rivers (Figure 3a) and strong variation in annual discharge (Figure 3b). Despite the small number of large floods, there was a chronic reduction in annual discharge during the Millennium Drought across all rivers (Figure 3b).

In all rivers, the random year effect from the NULL 2 model was correlated with annual discharge (Figure 3c). Some interannual variation detected in the year random effects did not correlate well with our two extrinsic covariates, indicating that: (a) factors in addition to annual discharge and temperature contribute to interannual growth dynamics of Murray cod (e.g. density-dependence); and/or (b) flow and temperature covariates additional to those specified in our parameterisations (i.e.. annual discharge and annual temperature; Appendix S3) influence interannual growth dynamics of Murray cod.

Our fitted growth model highlighted the stage-specificity of Murray cod growth dynamics, and some clear effects of annual discharge that were consistent across rivers (Figure 3d). For late juveniles and adults, growth rates were reduced during drought but increase sharply during floods (Figure 3d). Early juvenile growth was suppressed when annual discharge departed strongly from the long-term mean (Figure 3d).

Growth of early juvenile Murray cod peaked at intermediate annual discharge (50th percentile or median of annual discharge; Figure 4; top row). This unimodal response of early juvenile growth to annual discharge was consistent across rivers (Figure 4; top row). Growth of late

juvenile and adult Murray cod increased almost monotonically with annual discharge (Figure 4; rows 2 and 3). Mean growth rates of all life-stages varied among rivers (Figure 4). Uncertainty generated by the interaction flow has with temperature stochasticity was small relative to that generated by statistical uncertainty (Figure 4). Despite the combined contributions of both environmental and statistical uncertainty, there was strong variation in the predicted growth among annual discharge levels, indicated by separation of growth interquartile ranges (IQRs) within rivers (Figure 4).

The temperature at which peak Murray cod growth occurred increased with age (Figure 5). 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 5). The effects of annual temperature on growth, as well as the contributions of different forms of uncertainty, were consistent across rivers (Figure 5). At high annual temperatures, most of the uncertainty around the effect of temperature on growth was generated by statistical uncertainty (Figure 5). At lower annual temperatures, however, the interaction annual temperature has with variability in annual discharge often generated as much, or more, uncertainty around the effect of annual temperature on growth as statistical uncertainty (Figure 5).

4 DISCUSSION

The growth dynamics of Murray cod were driven by interactions between factors extrinsic and intrinsic to the population. Annual growth of Murray cod showed significant, curvilinear, stage-specific responses to an interaction between annual discharge and air temperature. Annual discharge and temperature accounted for a larger percentage of age-specific growth variation in adults (~45%) compared to late (~30%) and early (~20%) juveniles. Interannual variation in discharge had a stronger effect on growth dynamics than interannual variation in temperature. Growth of early juveniles (1+ and 2+) exhibited a unimodal relationship with annual discharge, peaking near median annual discharge. Growth of late juveniles (3+ to 5+) and adults (> 5+) increased with annual discharge, with the rate of increase being particularly high in adults. Unimodal relationships between growth and annual temperature were evident across all life-stages. Contrary to our hypothesis and the TSR, the air temperature at which maximum growth occurred increased with age, such that growth was maximal at ca. 23 °C,

24 °C and 26-27 °C in early juveniles, late juveniles and adults, respectively. An analysis of uncertainty showed that the effects of each covariate—annual discharge and temperature—were generally 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. A strong and significant first-order autocorrelation term indicated that the growth dynamics of Murray cod are characterised by lagged temporal responses to environmental change.

4.1 Stage-specific flow and temperature impacts

The unimodal relationship between annual discharge and growth of early juvenile Murray cod was consistent across rivers. Other studies have reported either a positive (Davidson et al., 2010; Nislow et al., 2004; Spurgeon & Pegg, 2017) or a negative (Jensen & Johnsen, 1999; Nunn, Cowx, Frear, & Harvey, 2003) relationship between growth of early juvenile fishes and river discharge, suggesting that responses are species-specific and/or dependent on where along the full domain of flow variability data is collected from. One of the challenges in identifying the hydrological and/or hydraulic mechanisms driving annual growth dynamics is the temporal resolution of the data. That is, annual growth of an individual is the result of the environmental conditions experienced by that individual over the entire growth year.

If growth is highest during years of median annual discharge, what were the hydrological/hydraulic characteristics of the riverscape during such years? Within our dataset there was a positive relationship between annual discharge during a growth year and the distribution of daily discharges within that year such that, for example, years of median annual discharge were characterised by many days of intermediate daily flow rates (Appendix 6). With this relationship between annual and daily discharges in mind, we offer the following hypothesis—comprised of two parts—to explain the unimodal relationship between annual discharge and growth of cod during the early juvenile stage: (a) slackwater area exhibits a unimodal relationship with river flows, peaking at median annual discharge; and (b) slackwaters represent the most productive foraging habitat for Murray cod during the early juvenile stage.

Slackwaters are hydraulic ‘microhabitats’ within ‘channel units’ (following Fausch, Torgersen, Baxter, & Li, 2002) characterised by shallow depths and low velocities (Vietz, Sammonds, & Stewardson, 2013). 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 while Vietz et al. (2013) reported that slackwater extent was maximised at intermediate flows. Slackwaters are productive foraging habitats for riverine fishes during their early life history (Humphries et al., 2020). This may be at least partly due to slackwaters supporting high densities of micro- and macro-invertebrates (Ning, Nielsen, Paul, Hillman, & Suter, 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). 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, assuming slackwaters are a particularly productive foraging habitat for Murray cod during early life history.

In contrast with early juveniles, growth of late juvenile and adult Murray cod increased with annual discharge in a mostly linear manner. This result generalises the inferences of Tonkin et al. (2017), who found that growth of Murray cod in a single river segment increased in years characterised by high spring discharge. 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; Wainwright & Richard, 1995; Winemiller, 1989). Given this general shift in diet, growth of larger adult Murray cod may increase most 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 pulses of energy through the food web (Balcombe & Arthington, 2009; Bayley, 1991; Benke, 2001; McInerney et al., 2017; Winemiller, 2004).

There is growing evidence for a shift in the size composition of ectothermic populations towards smaller individuals as habitats warm (Audzijonyte et al., 2020). According to the TSR, a mechanism that may underpin this shift is for warming to accelerate growth and maturation of juveniles, but retard growth of adults (Ohlberger, 2013). The temperature-dependence of Murray cod growth varied across stages in the direction opposite to that predicted by the TSR; the air temperatures at which maximum growth occurred increased with age. Thus, given our data and model, we predict faster adult growth but slower juvenile

growth of Murray cod in a warming world (see Implications for Management). Daufresne et al. (2009) reported reduced growth of young-of-year cyprinids as a function of long-term warming in French rivers, but did not consider adult growth dynamics. Huss et al. (2019) studied long-term concurrent growth dynamics of juvenile and adult Eurasian perch (*Perca fluviatilis*) exposed to experimental warming. They demonstrated that juvenile growth increased with temperature, but that adult growth and age at maturity did not decline with temperature. Consequently, our study along with that of Huss et al. (2019) and Daufresne et al. (2009) confer little support for faster juvenile / slower adult growth as a mechanism underpinning observed shifts in the size composition of fish populations.

One could suggest that the result reported here of a positive relationship between optimal air temperature for growth and age is counterintuitive; several physiological experiments—like those upon which the TSR is founded (Atkinson, 1994)—have shown that thermal performance curves of juveniles have higher thermal optima than those of adults (Messmer et al., 2017; e.g. Peck et al., 2009). Indeed, experimental estimates of the stage- and temperature-dependence of fish growth also report a negative relationship between size or stage and the thermal optima for growth (Björnsson & Steinarsson, 2002; Duston, Astatkie, & MacIssac, 2004; Morita, Fukuwaka, Tanimata, & Yamamura, 2010). Importantly, such estimates were obtained under maximum rations and tightly controlled conditions to isolate the intrinsic effects of temperature on growth; intrinsic effects being the direct effects of temperature on the physiological mechanisms controlling conversion of energy intake into somatic growth. By contrast, *in situ* or field studies of temperature-dependent growth incorporate both intrinsic and extrinsic effects of temperature on growth. Extrinsic effects of temperature on somatic growth of consumers include the effects temperature has on, for example, productivity and composition of the prey community (Hood et al., 2018; Nelson et al., 2017; Yvon-Durocher, Montoya, Trimmer, & Woodward, 2011) and behavioural interactions between the consumer and its prey and/or predators (Grigaltchik, Ward, & Seebacher, 2012). Furthermore, non-thermal factors may restrict certain life stages to sub-optimal habitats in the wild (e.g. predators restricting juveniles to refuges), further complicating the mapping of environmental temperature to growth. Using the terminology of Hutchinson (1957), controlled laboratory experiments (e.g. Peck et al. 2009, Messmer et al. 2017) estimate the growth axes of the *fundamental thermal niche*, whilst field studies like ours estimate the growth axes of the *realised thermal niche* (Kearney, 2006). The mapping of the fundamental thermal niche to the realised thermal niche is a function of both the intrinsic

and extrinsic effects of temperature, and the non-thermal constraints mentioned above (Holt, 2009).

Discordance between lab- and field-based estimates of the stage and temperature-dependence of fish growth have been documented for Atlantic cod (Righton et al., 2010) and salmonids (Jonsson & Jonsson, 2009). With respect to Murray cod, Svozil et al. (2018) determined the effect of temperature on growth of larval Murray cod, but there have been no experiments on the stage- and temperature-dependent growth of Murray cod beyond their first year of life. We cannot, therefore, contrast our estimates of the growth axes of the Murray cod realised thermal niche with those of their fundamental thermal niche. Numerous hypotheses could be offered as to why the temperatures at which peak juvenile growth occurred were relatively lower than anticipated (or, conversely, why the temperatures at which adult growth occurred were relatively higher than anticipated). For example, Elliott and Hurley (2000) showed that the optimal temperature for brown trout growth declines as food becomes scarce. With respect to the present study, perhaps food for early juvenile Murray cod was in short supply, depressing the temperature at which optimal growth occurred. In any case, research programmes that meld multiple approaches to estimating both fundamental and realised thermal niches are required to more confidently forecast the stage-dependent effects of thermal change, and decipher the mechanisms underpinning patterns such as the TSR.

4.2 Implications for management

Our analysis showed that the effects of annual discharge were robust to uncertainty generated by 30 years of observed, interannual variation in temperature—variation that included a clear, gradual warming trend in all systems studied. That is, the interaction between annual discharge and temperature was not so strong as to erode our confidence in qualitative, near-future predictions we may make concerning the effect of river flows on Murray cod growth.

The stage-specific response of Murray cod to annual discharge indicates that no single magnitude of annual discharge is optimal for populations. Our results add further support to the maintenance and/or restoring of flow variability in riverine ecosystems; not just within years, but among years also (Bunn & Arthington, 2002; Poff et al., 1997). Years of median annual discharge may promote growth of early juvenile Murray cod, hence recruitment, while years containing flood pulses may promote growth of adult Murray cod. Years of very low

annual discharge, as experienced during the Millenium Drought, suppress growth rates of all cod life-stages. It follows that in the case of the Murray cod, designing flow regimes (sensu Acreman et al., 2014) to benefit an iconic species presents both an opportunity and a challenge to river managers. The opportunity is that river managers can exploit natural variability in the availability of water for the environment. For example, in dry years when there is insufficient environmental water to achieve high environmental flows, aiming for intermediate flows to promote growth and recruitment of an iconic species is a defensible and achievable management objective.

The challenge has three components, with the first of those components being more surmountable than the others. First, river managers must build interannual heterogeneity into water plans. Second, given adult Murray cod growth reaches a maximum when annual discharge is also at its maximum, floods are likely a key component of the flow regime for Murray cod. River managers, however, are often constrained to delivering flows that do not exceed the bankfull threshold, to avoid damaging human infrastructure on floodplains (Bond et al., 2014; Stoffels, Clarke, Rehwinkel, & McCarthy, 2013). Indeed, river regulation in the MDB has greatly reduced the frequency and magnitude of floods (Sims, Chariton, Jin, & Colloff, 2012) and by 2030 we may expect a further 13% decrease (cf. 2009) in total discharge under a ‘medium-severity’ climate forecast (Kirby, Mainuddin, Ahmad, & Gao, 2013). Third, prolonged periods of low annual discharge will suppress cod growth, highlighting the need for environmental flows during drought. Again, this will be a challenge under the future MDB climate, which is forecast to experience more frequent and severe droughts (CSIRO and Bureau of Meteorology, 2015).

As was the case for annual discharge, the effects of changes in annual temperature on Murray cod growth were stage-specific, and generally robust to uncertainty generated by the interaction annual temperature had with temporal stochasticity in discharge. The annual temperature baseline for our four rivers is ca. 23.4 °C (baseline period: 1961-990, following Intergovernmental Panel on Climate Change 2013; Appendix 2). According to the IPCC’s (2013) Representative Concentration Pathways (RCPs), by 2090, increases in mean air temperatures within the MDB are forecast to be between 1.5 and 2.9 °C under RCP4.5 (low-emission, ‘best-case’ scenario; stabilising CO₂ at 540 ppm by end of 21st century), and 2.9

and 5.3 °C under RCP8.5 ('business as usual' high-emission scenario; CO₂ reaching 940 ppm by end of 21st century) (Ekström et al., 2015; Timbal et al., 2015; Watterson et al., 2015). These forecasts imply that, by 2090, the mean maximum annual air temperatures of our study systems will be between 24.9 °C and 28.7 °C. Other recent studies have highlighted the potential for these scenarios to impact on native fish growth and distribution patterns within the MDB (Galego de Oliveira et al., 2019; John R. Morrongiello et al., 2011; J. R. Morrongiello et al., 2011). According to our data and model, growth rates of juvenile Murray cod are optimal under IPCC baseline climatic conditions (23-24 °C), then decline as annual temperature warms. If we assume stationarity of the Murray cod thermal niche, as well as the temperature-dependence of all food web processes, then we can expect growth of juveniles to decline under the IPCC RCP4.5 and RCP8.5 scenarios. Contrasting with juveniles, our model and data indicate that growth rates of adults are below optimal under baseline climatic conditions, and may increase as the climate warms under the RCP4.5 and RCP8.5 scenarios.

These divergent responses of life-stages to temperature generate considerable uncertainty as to the effects of changing thermal regimes on the growth dynamics of Murray cod. In light of this uncertainty and our observation that annual discharge has a stronger effect on Murray cod growth than annual temperature, we suggest that the forecast reduction in the availability of freshwater within the MDB (Sims et al. 2012, Kirby et al. 2013, Colloff et al. 2016) presents a more immediate and greater climate-driven threat to Murray cod growth dynamics than increases in annual mean temperature *per se*. This is not to say, however, that altered thermal regimes pose less of a climate-driven challenge to resource managers than altered river flows. Altered thermal regimes clearly present a great challenge to resource managers, as demonstrated by recent mass fish mortality events associated with heat waves (Harris et al. 2018, Vertessy et al. 2019). Clearly, effects of climate change on both river flows and thermal regimes will compound the long-standing threat to riverine populations posed by damming and water abstraction. In light of this conclusion, an outstanding research challenge is to integrate the effects of flow-temperature interactions on multiple population processes, towards identification of pathways that are most threatening to population dynamics (e.g. cessation of recruitment during prolonged low-flow periods) and, consequently, the prioritisation of management interventions.

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Data Availability Statement

Restrictions apply to the availability of these data, which were used under license for this study. Data are available from the authors with the permission of NSW Fisheries.

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TABLES

Table 1. Description of the three classes of Generalised Additive Mixed Models fitted to increment width data.

Model name	Formula	Description
<i>Spatial, intrinsic and year effects</i>		
Null 1	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + \varepsilon_{tij},$ $j = 1, \dots, n, \quad i = 1, \dots, n_j, \quad t = 1, \dots, n_{ij}$ $\alpha_j \sim N(0, \sigma_1^2), \quad \alpha_{ij} \sim N(0, \sigma_2^2), \quad \varepsilon_{tij} \sim N(0, \sigma^2).$	Increment width (G_{tij} ; mm) of Individual i 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) + deviation induced by effect of individual i nested within River j (α_{ij}) + the effect of age during year t of individual i in River j (included as a smoother, $f(A_{tij})$) + error. The factor α is fixed while α_j and α_{ij} are random. Age is, of course, a fixed factor. 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	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + \alpha_{tj} + f(A_{tij}) + \varepsilon_{tij}$, $j = 1, \dots, n, \quad i = 1, \dots, n_j, \quad t = 1, \dots, n_{ij}$ $\alpha_j \sim N(0, \sigma_1^2), \quad \alpha_{ij} \sim N(0, \sigma_2^2), \quad \alpha_{tj} \sim N(0, \sigma_3^2), \quad \varepsilon_{tij} \sim N(0, \sigma^2)$.	As above, but now containing crossed random factors; the random effect of growth year t is nested within river system j .
<i>Spatial, intrinsic and extrinsic effects</i>		
E1	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + f(F_{tij}, A_{tij}) + \varepsilon_{tij}$, $j = 1, \dots, n, \quad i = 1, \dots, n_j, \quad t = 1, \dots, n_{ij}$ $\alpha_j \sim N(0, \sigma_1^2), \quad \alpha_{ij} \sim N(0, \sigma_2^2), \quad \varepsilon_{tij} \sim N(0, \sigma^2)$.	Null 1 + curvilinear effects induced by the interaction between standardised discharge and age.
E2	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + f(T_{tij}, A_{tij}) + \varepsilon_{tij}$, $j = 1, \dots, n, \quad i = 1, \dots, n_j, \quad t = 1, \dots, n_{ij}$ $\alpha_j \sim N(0, \sigma_1^2), \quad \alpha_{ij} \sim N(0, \sigma_2^2), \quad \varepsilon_{tij} \sim N(0, \sigma^2)$.	Null 1 + curvilinear effects induced by the interaction between mean maximum daily temperature and age.
E3	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + f(F_{tij}, A_{tij}) + f(T_{tij}, A_{tij}) + \varepsilon_{tij}$, $j = 1, \dots, n, \quad i = 1, \dots, n_j, \quad t = 1, \dots, n_{ij}$ $\alpha_j \sim N(0, \sigma_1^2), \quad \alpha_{ij} \sim N(0, \sigma_2^2), \quad \varepsilon_{tij} \sim N(0, \sigma^2)$.	Null 1 + the curvilinear effects of the interaction between standardised discharge and age, and the interaction between age and mean maximum daily temperature. 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	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + f(F_{tij}, A_{tij}) + f(T_{tij}, A_{tij}) + f(F_{tij}, T_{tij}, A_{tij}) + \varepsilon_{tij}$, $j = 1, \dots, n, \quad i = 1, \dots, n_j, \quad t = 1, \dots, n_{ij}$ $\alpha_j \sim N(0, \sigma_1^2), \quad \alpha_{ij} \sim N(0, \sigma_2^2), \quad \varepsilon_{tij} \sim N(0, \sigma^2)$.	As E3, but also 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.
<i>Spatial, intrinsic and extrinsic effects, including temporal autocorrelation</i>		
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, but with temporal autocorrelation.

Table 2. Performance statistics for the models in the candidate set, sorted in increasing order by their Akaike Information Criteria (AIC; decreasing log-likelihood (Log(L)). $\Delta_i = \text{AIC}_i - \min(\text{AIC})$ 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 & Anderson 2002).

Model name	AIC	log(L)	Δ_i	w_i
E8	-13898.96	6967.48	0.00	1.00
Null 2	-13868.46	6941.23	30.50	0.00
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 1	-8004.02	4006.01	5894.94	0.00

Table 3. Parameter estimates of the final model of Murray cod growth. The first-order temporal autocorrelation is given by ρ . NSE is the Nash-Sutcliffe Equilibrium; a measure of predictive accuracy on independent data. Effective degrees of freedom (edf) is an indicator of how curvilinear a smoother is (edf = 1 indicates a straight line, while edf > 8 indicates the smoother is highly non-linear).

$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + f(F_{tij}, A_{tij}) + f(F_{tij}, T_{tij}, A_{tij}) + \varepsilon_{tij}$ $j = 1, \dots, n, \quad i = 1, \dots, n_j, \quad t = 1, \dots, n_{ij}$ $\alpha_j \sim N(0, \sigma_1^2), \quad \alpha_{ij} \sim N(0, \sigma_2^2), \quad \varepsilon_{ij} \sim N(0, \sigma^2)$		$\text{cor}(\varepsilon_s, \varepsilon_t) = \begin{cases} 1 & \text{if } s = t \\ \rho^{ t-s } & \text{else} \end{cases}$
$R^2 = 0.82$		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

FIGURE LEGENDS

Figure 1. Magnitudes of the age-specific, combined effects of annual discharge and temperature on Murray cod growth. A smoother (+/- 95% CI) has been added to highlight the general change in effect size with age.

Figure 2. Relative effect sizes of annual discharge and annual temperature on interannual dynamics of Murray cod growth. Predictions include fixed effects and the random effect of river system. Transparency of the columns was weighted by relative sample size within each river; the more transparent the smaller the sample size (see Appendix S1).

Figure 3. 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 major floods. Long-term mean discharge denoted by $y = 0$ in (b). The random effects of year (c; +/- 95% CI) and the fitted model (d; +/- 95% CI) are presented 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.

Figure 4. 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.

Figure 5. 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

1096 in annual discharge ('Discharge'; a form of environmental uncertainty), and environmental and
1097 statistical uncertainty ('Discharge + Statistical'). Annual temperatures are in degrees Celsius.

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