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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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35

36

37 **Abstract**

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

62

63 **Keywords:** discharge; climate change; fish; flow; growth; recruitment; river; Temperature Size Rule; thermal
64 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

98 same long-term hydrological series (but see Morrongiello, Walsh, Gray, Stocks, & Crook,
99 2014; Z. Tonkin et al., 2017). With respect to temperature, we know that the thermal
100 performance curves of an ectotherm may vary through ontogeny (Peck, Clark, Morley,
101 Massey, & Rossetti, 2009), yet our understanding of the direction and magnitude of that
102 variation is surprisingly poor for all ectotherms (Ohlberger, 2013; Sinclair et al., 2016).
103 Laboratory experiments generally indicate that juveniles ($\geq 1+$ age) of fishes with medium-
104 high longevity tend to have ‘warm-shifted’ thermal performance curves relative to adults,
105 perhaps conferring juveniles greater resilience to warming than adults (Clark et al., 2013;
106 Messmer et al., 2017; Peck et al., 2009; Peck, Souster, & Clark, 2013). Surprisingly,
107 however, our knowledge of how temperature interacts with ontogenetic stage to affect growth
108 curves of fishes with medium-high longevity is poor, even for species of high socioeconomic
109 importance that have been extensively studied (e.g. Jonsson & Jonsson, 2009). Faster juvenile
110 growth and maturation, coupled with retardation of adult growth under warming is a pattern
111 expected under the Temperature Size Rule (TSR; Atkinson, 1994; Audzijonyte et al., 2019).
112 Empirical tests of the TSR have mostly come in the form of documented shifts in population
113 size composition towards smaller individuals as habitat temperature warms (Baudron,
114 Needle, Rijnsdorp, & Tara Marshall, 2014; Daufresne, Lengfellner, & Sommer, 2009; Horne,
115 Hirst, & Atkinson, 2017; van Rijn, Buba, DeLong, Kiflawi, & Belmaker, 2017). Although
116 such compositional shifts are an emergent result of the mechanisms proposed under TSR,
117 other non-thermal causes may produce the same shifts, and so there is a need for studies of
118 the concurrent, stage-specific growth dynamics of ectotherms, to test the applicability of the
119 TSR to wild populations (Audzijonyte et al., 2019; Lindmark et al., 2018; Ohlberger, 2013).
120
121 Here we used a novel data set spanning 34 years and multiple sub-catchments covering ca.
122 400,000 km² across Australia’s Murray-Darling Basin (MDB) to improve our understanding
123 of how the growth dynamics of an iconic apex predator, Murray cod (*Maccullochella peelii*,
124 Mitchell 1838; Percichthyidae), responds to interannual dynamics of flow and temperature.
125 Long-lived apex predators are of global interest due to their top-down, often cascading,
126 effects on multiple species in the food web (Estes et al., 2011; Ripple et al., 2014). There
127 have also been recent calls for an improved understanding of the population dynamics of
128 freshwater ‘megafauna’ species (freshwater animals that can reach a body mass ≥ 30 kg),
129 which have traits conferring high susceptibility to the degradation of freshwater ecosystems,
130 and are therefore of global conservation concern (He et al., 2019). The Murray cod has the
131 physiological and life-history traits of a freshwater megafauna species (He et al., 2019), and

132 so knowledge of its response to flow and thermal regimes will facilitate improved
133 management of freshwater megafauna. We partitioned a mix of ‘intrinsic’ and ‘extrinsic’
134 factors that may drive growth dynamics (Morrongiello & Thresher, 2015). In our case,
135 intrinsic sources of variance in growth essentially refer to the influence of phenotype and
136 genotype; the effects of age/stage and the individual. Extrinsic sources of variance in growth
137 refer to environmental covariates that vary in space and time; flow and temperature are of
138 primary interest, but to facilitate general, population-wide inference we accounted for the
139 effect of river system on the sub-populations studied. We expected the growth response of
140 Murray cod to be a unimodal function of temperature (Kingsolver, 2009; Wootton, 2011),
141 and that the growth curve of juveniles would be warm-shifted relative to adults, consistent
142 with the TSR (Atkinson, 1994). The literature concerning the response of fish growth to river
143 flows is not sufficiently well developed to offer meaningful stage-specific hypotheses.
144 However, we generally anticipated a positive relationship between discharge and Murray cod
145 growth, consistent with recent studies of other species and the Flood Pulse Concept (Izzo et
146 al., 2016; Junk, Bayley, & Sparks, 1989; Z. D. Tonkin, King, Robertson, & Ramsey, 2011).

147

148 **2 MATERIALS AND METHODS**

149 **2.1 Study species**

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

157

158 **2.2 Data collation**

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

162

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

165 Collections were made from a river segment ca. 100–400 km in length within each river
166 system. Photographs of the sagittal section of each otolith were imported into Zen 2.3 Blue
167 Edition (Carl Zeiss Microscopy GmbH, 2011) microscopy software for precise digital
168 measurements. The widths of annual growth increments were measured perpendicular to the
169 axis of growth along a transect line that was established on the proximal axis, drawn from the
170 core to the outer edge (following Morrongiello, Crook, King, Ramsey, & Brown, 2011). Fish
171 were assigned a nominal birthdate of October 1st (approximate hatch date of larval cod, on the
172 average) and annual growth increments were assigned ‘growth year’ t (such that growth year
173 t is 01/10/ t to 30/09/ $t+1$; note that much of the flow contributing to growth year t comes from
174 calendar year $t+1$). Capture date was known for all individuals, enabling us to assign growth
175 years and ages to each increment (Appendix S1).

176

177 Daily discharge (ML d^{-1}) data were obtained from 12 gauges within study segments (Table
178 S2). Air temperature was used as a surrogate for water temperature due to the paucity of
179 water temperature logging stations throughout the MDB (Table S2). Use of air temperature as
180 a proxy for water temperature was valid for two reasons: First, in our case it was not essential
181 to develop a model to infer or predict the effects of absolute water temperature. Second, river
182 water temperature is an increasing function of air temperature, and air temperature explains
183 the majority of variance in water temperature in rivers like the ones studied here, especially
184 when temperature data has an annual resolution (Mohseni, Stefan, & Erickson, 1998; van
185 Vliet, Ludwig, Zwolsman, Weedon, & Kabat, 2011; Webb, Clack, & Walling, 2003). Further
186 justification is provided in Appendix S2. Air temperatures were paired with a discharge
187 gauge by selecting the climate logging station closest to the discharge gauge.

188

189 We did not have information about the movement history of individuals within rivers, so we
190 made no attempt to pair individual otoliths with individual gauges at a fine spatial resolution.
191 Instead, for each of the five rivers we generated a daily discharge time series that applies to
192 each river as a whole. As such, any inference concerning the effects of discharge on growth
193 pertains to mean flows moving through a river, not individual reaches or anabranches
194 (Appendix S2). This approach was supported as pairwise correlations of the mean annual
195 discharges between gauges within rivers were significantly positive (Table S3).

196

197 **2.3 Model parameterisation, selection and testing**

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

204

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

213

214 For this analysis we sought simple model parameterisations of extrinsic factors that captured
215 how coarse interannual changes in the flow and thermal state of rivers drive growth dynamics
216 of Murray cod. We examined the effects of two fixed covariates on growth: mean annual
217 standardised discharge in growth year t (F_t ; hereafter '*annual discharge*'), and annual mean
218 maximum daily air temperature (T_t ; hereafter '*annual temperature*'). Other hydrological and
219 temperature covariates were considered but these were collinear and so were not included
220 (Appendix S3). Annual discharge should be positively related to the volume of foraging
221 habitat available to Murray cod. Further, this positive relationship is likely nonlinear, such
222 that beyond some threshold of annual discharge, the surface area of river-floodplain habitat
223 inundated increases exponentially, as flows spill out onto anabranches, benches and other
224 floodplain habitats, increasing not only habitat but production of food resources (Benke,
225 2001; McInerney, Stoffels, Shackleton, & Davey, 2017). Being ectotherms, temperature also
226 has a strong influence on fish growth, and hence was included in the models (Jobling, 1996).

227

228 Graphical examination of the relations between covariates and increment widths showed that
229 curvilinear relations were common. These curvilinear relationships had forms that were
230 unlikely to be neatly described by low-order polynomial terms (e.g. quadratics), especially in

231 the multilevel context, where parameters of, say, quadratic terms were likely to vary among
232 levels of random factors. In light of these observations we chose to use Generalised Additive
233 Mixed Models (GAMMs; S. N. Wood, 2017) for modelling G as a function of covariates.
234 The set of 10 candidate GAMMs is described in Table 1.

235
236 There were three classes of model, each of which partitioned different components of
237 variance in G : (1) Null models isolating the contributions of intrinsic factors individual and
238 age, and the extrinsic impacts of river system and year on G ; (2) four models that added the
239 extrinsic factors of primary interest in this paper—effects of annual discharge and
240 temperature; (3) as for (2), but including temporal autocorrelation in G (Table 1). The last
241 class of models was parameterised to account for temporal autocorrelation amongst residuals,
242 as significant temporal autocorrelation can affect inferences if unaccounted for (Zuur, Ieno,
243 Walker, Savaliev, & M., 2009). In addition, the presence of strong temporal correlation may
244 indicate multi-year biological processes are influencing growth rates, but which are
245 unaccounted for within the fixed components of models.

246
247 The candidate model set was mostly nested, such that simpler models were subsets of more
248 complex models. The exception was Null 2, which included a crossed random factor to
249 account for the effect of year on growth variability within rivers (Table 1). The year effect in
250 Null 2 enabled us to include a factor that might account for all drivers of interannual variation
251 in growth, not just those of discharge and temperature. As such, Null 2 makes for a useful
252 comparison with Models E1-E8; if Null 2 has a high probability of being the most likely
253 model in the candidate set, given the data, then that indicates factors other than flow and
254 temperature may be having a significant influence on the interannual growth dynamics of
255 cod.

256
257 Null 2 was not a subset of E1-E8 due to limitations of the various R packages used for
258 GAMMs. Given our analysis is a time series analysis, accounting for possible temporal
259 autocorrelation was considered a priority. The `mgcv` package enables inclusion of
260 autocorrelation terms and was used for estimating the parameters of Null 1 and E1-E8 (S. N.
261 Wood, 2017). However, the `mgcv` package does not easily accommodate crossed random
262 factors so the `gamm4` package was used to fit Null 2 to the data (S. Wood & Scheipl, 2017).
263 Generalised cross-validation was implemented to ensure individual smooth terms were not
264 overfitted to data (S. N. Wood, 2017).

265

266 Selecting among competing mixed-effects models is an area of active statistical research and
267 there is currently no consensus on which approach performs best (Bolker et al., 2009; Wang
268 & Gelman, 2015). We used an information-theoretic approach for model selection (Burnham
269 & Anderson, 2002), based on the Akaike Information Criterion (AIC; Akaike, 1974). We also
270 trialled a k -fold cross-validation approach to model selection (Hastie, Tibshirani, &
271 Friedman, 2009), but found it a less sensitive tool for mixed-effects model selection than
272 AIC, following the more general observation of Wang and Gelman (2015). The objective of
273 this analysis was to yield general inferences and predictions concerning how Murray cod
274 growth responds to discharge and temperature. We therefore tested the predictive accuracy of
275 the final GAMM using data independent to that used for parameter estimation. Model
276 selection was carried out using ca. 80% of the global data set (the training data), reserving the
277 remaining ca. 20% of the data for model testing (the testing data). We wished to test the
278 accuracy of predictions about how individual fish respond to discharge and temperature, so
279 we ensured no ‘leakage’ of data from individual fish across testing and training data sets
280 (using `groupdata2`; Olsen, 2017). Nash-Sutcliffe Efficiency (NSE; Nash & Sutcliffe, 1970)—
281 which is essentially the coefficient of determination estimated using the testing data—was
282 used to determine predictive accuracy. NSE measures how close the observed and predicted
283 values within the testing data are to the 1:1 line. NSE values range from $-\infty$ to 1. An NSE of
284 1 corresponds to a perfect match between predictions and the observed data, an NSE of 0
285 indicates that the model predictions are as accurate as the mean of the observed data; and an
286 NSE less than 0 indicates that the observed mean is a better predictor than the model.

287

288 **2.4 Analysis of final model and uncertainty**

289 Age typically accounts for most of the variance in growth of long-lived fishes (Morrongiello
290 & Thresher, 2015). To isolate and quantify the magnitudes of the combined effects of annual
291 discharge and temperature, we estimated age-specific magnitude of covariate effects as the
292 range of fitted values (fixed effects + random effect of river) within an age (R_f), expressed as
293 a percentage of the range of raw increment widths within that age (R_o) (e.g. Izzo et al., 2016):
294 $(R_f/R_o) \cdot 100$. We also determined the relative effect sizes of annual discharge and
295 temperature on Murray cod growth. We used the final model to predict the range in growth of
296 three life-stages (see Results) as a function of one covariate while fixing the value of the
297 other at its median value, within each respective river. When estimating the effect size of a

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

301

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

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

315 Two fixed, extrinsic covariates were the focus of this uncertainty analysis: annual discharge
316 and annual temperature. At its core the algorithm for this uncertainty analysis involves
317 predicting growth of Murray cod at a set of fixed values of one of these covariates while
318 simulating environmental uncertainty (plus statistical uncertainty) in the other covariate. The
319 output of this analysis was a set of boxplots describing distributions of predicted Murray cod
320 growth rates. Appendix S4 explains this analysis in detail.

321

322 **3. RESULTS**

323 Our database comprised 4124 growth increments from 961 Murray cod otoliths.

324 Biochronology lengths ranged from 9 to 34 years among rivers (spanning 1981 – 2014), with
325 growth estimates from ages 1+ through to 28+ (Appendix S1).

326

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

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

334

335 The fixed terms of Model E8 included a global intercept, and four smooth terms: (1) the
336 effect of age; (2) the interaction between age and annual discharge; (3) the interaction
337 between age and temperature; and (4) the interaction between age, annual discharge and
338 temperature (Table 1). There was weak evidence for a significant effect of the third smooth
339 term, the interaction between age and temperature ($F = 0.57$; $P = 0.72$), so that term was
340 dropped from Model E8 to yield the final model, presented in Table 3 ($AIC = -13897$; $\log(L)$
341 $= 6966$). This final model fit the data well, with generally homogeneous residuals and no bias
342 evident in the fit (Appendix S5). Predictive accuracy, as measured using NSE, was 0.79,
343 which was comparable with the variance explained in the training data by the model (Table
344 3).

345

346 One of the most notable features of the final model's random component was the high
347 temporal autocorrelation among residuals through time. The estimated value of ρ was 0.49,
348 meaning that, after we accounted for the variance explained by flow and temperature
349 covariates, residual variation in Murray cod growth was significantly correlated among years
350 (Table 3). Variation in random intercepts among individuals within rivers was low, but
351 variation in random intercepts among rivers was approximately half that of residual error
352 (Table 3). The intraclass correlation coefficient (Gelman & Hill, 2007) for growth among
353 individuals within rivers was 0.18, while the correlation in increment widths within
354 individuals, within rivers was also 0.18 (identical at two significant digits due to the very
355 small value of σ_2). Growth rate declined with age (Table 3; Appendix S1) and the global R^2
356 of the model including only spatial and intrinsic effects of age and individual (Null 1) was
357 0.80. The R^2 of the final extrinsic model was 0.82 (Table 3).

358

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

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

373

374 The temporal domain of our training data (1981–2014) encompassed two major floods and
375 the Millennium Drought ca. 2000–2010 (van Dijk et al., 2013) (Figure 3). It included a
376 warming trend across all rivers (Figure 3a) and strong variation in annual discharge (Figure
377 3b). Despite the small number of large floods, there was a chronic reduction in annual
378 discharge during the Millennium Drought across all rivers (Figure 3b).

379

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

387

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

393

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

397 juvenile and adult Murray cod increased almost monotonically with annual discharge (Figure
398 4; rows 2 and 3). Mean growth rates of all life-stages varied among rivers (Figure 4).
399 Uncertainty generated by the interaction flow has with temperature stochasticity was small
400 relative to that generated by statistical uncertainty (Figure 4). Despite the combined
401 contributions of both environmental and statistical uncertainty, there was strong variation in
402 the predicted growth among annual discharge levels, indicated by separation of growth
403 interquartile ranges (IQRs) within rivers (Figure 4).

404
405 The temperature at which peak Murray cod growth occurred increased with age (Figure 5).
406 The annual temperature corresponding with peak growth was predicted to be approximately
407 23 °C, 24 °C and 26-27 °C in 1+, 5+ and 11+ individuals, respectively (Figure 5).
408 The effects of annual temperature on growth, as well as the contributions of different forms
409 of uncertainty, were consistent across rivers (Figure 5). At high annual temperatures, most of
410 the uncertainty around the effect of temperature on growth was generated by statistical
411 uncertainty (Figure 5). At lower annual temperatures, however, the interaction annual
412 temperature has with variability in annual discharge often generated as much, or more,
413 uncertainty around the effect of annual temperature on growth as statistical uncertainty
414 (Figure 5).

417 **4 DISCUSSION**

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

430 24 °C and 26-27 °C in early juveniles, late juveniles and adults, respectively. An analysis of
431 uncertainty showed that the effects of each covariate—annual discharge and temperature—
432 were generally robust to (a) environmental uncertainty generated by the interaction one
433 covariate had with stochastic temporal variation in the other, as well as spatial variation
434 among rivers, and (b) statistical uncertainty generated by error in model parameter estimates.
435 A strong and significant first-order autocorrelation term indicated that the growth dynamics
436 of Murray cod are characterised by lagged temporal responses to environmental change.

437

438 **4.1 Stage-specific flow and temperature impacts**

439 The unimodal relationship between annual discharge and growth of early juvenile Murray
440 cod was consistent across rivers. Other studies have reported either a positive (Davidson et
441 al., 2010; Nislow et al., 2004; Spurgeon & Pegg, 2017) or a negative (Jensen & Johnsen,
442 1999; Nunn, Cowx, Frear, & Harvey, 2003) relationship between growth of early juvenile
443 fishes and river discharge, suggesting that responses are species-specific and/or dependent on
444 where along the full domain of flow variability data is collected from. One of the challenges
445 in identifying the hydrological and/or hydraulic mechanisms driving annual growth dynamics
446 is the temporal resolution of the data. That is, annual growth of an individual is the result of
447 the environmental conditions experienced by that individual over the entire growth year.

448

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

460

461 Slackwaters are hydraulic ‘microhabitats’ within ‘channel units’ (following Fausch,
462 Torgersen, Baxter, & Li, 2002) characterised by shallow depths and low velocities (Vietz,
463 Sammonds, & Stewardson, 2013). Price et al. (2012) showed that the surface area of

464 slackwater habitat in the main channel of a lowland river is eroded at high flow rates while
465 Vietz et al. (2013) reported that slackwater extent was maximised at intermediate flows.
466 Slackwaters are productive foraging habitats for riverine fishes during their early life history
467 (Humphries et al., 2020). This may be at least partly due to slackwaters supporting high
468 densities of micro- and macro-invertebrates (Ning, Nielsen, Paul, Hillman, & Suter, 2010).
469 Although we know little about ontogenetic diet shifts in Murray cod (Stoffels, 2013), micro-
470 and macro-invertebrates generally comprise the most important source of energy for
471 carnivorous riverine fishes during early ontogeny (Wainwright & Richard, 1995; Winemiller,
472 1989). Thus the unimodal relationship between early juvenile growth and annual discharge
473 may be a consequence of a similar relationship between annual discharge and slackwater
474 surface area, assuming slackwaters are a particularly productive foraging habitat for Murray
475 cod during early life history.

476

477 In contrast with early juveniles, growth of late juvenile and adult Murray cod increased with
478 annual discharge in a mostly linear manner. This result generalises the inferences of Tonkin
479 et al. (2017), who found that growth of Murray cod in a single river segment increased in
480 years characterised by high spring discharge. A common pattern seen in ram-suction feeding
481 carnivores, like Murray cod, is an ontogenetic shift from feeding on insects and small
482 crustaceans during early juvenile stages, through to piscivory and feeding on larger
483 crustaceans during late juvenile and adult stages (Amundsen et al., 2003; Wainwright &
484 Richard, 1995; Winemiller, 1989). Given this general shift in diet, growth of larger adult
485 Murray cod may increase most during years that coincide with high rates of production of
486 forage fishes and larger crustaceans. In river-floodplain systems, such years are usually
487 characterised by a flood pulse of some magnitude, whereupon rewetting of habitats higher in
488 the riverscape results in pulses of energy through the food web (Balcombe & Arthington,
489 2009; Bayley, 1991; Benke, 2001; McInerney et al., 2017; Winemiller, 2004).

490

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

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

507

508 One could suggest that the result reported here of a positive relationship between optimal air
509 temperature for growth and age is counterintuitive; several physiological experiments—like
510 those upon which the TSR is founded (Atkinson, 1994)—have shown that thermal
511 performance curves of juveniles have higher thermal optima than those of adults (Messmer et
512 al., 2017; e.g. Peck et al., 2009). Indeed, experimental estimates of the stage- and
513 temperature-dependence of fish growth also report a negative relationship between size or
514 stage and the thermal optima for growth (Björnsson & Steinarsson, 2002; Duston, Astatkie, &
515 MacIssac, 2004; Morita, Fukuwaka, Tanimata, & Yamamura, 2010). Importantly, such
516 estimates were obtained under maximum rations and tightly controlled conditions to isolate
517 the intrinsic effects of temperature on growth; intrinsic effects being the direct effects of
518 temperature on the physiological mechanisms controlling conversion of energy intake into
519 somatic growth. By contrast, *in situ* or field studies of temperature-dependent growth
520 incorporate both intrinsic and extrinsic effects of temperature on growth. Extrinsic effects of
521 temperature on somatic growth of consumers include the effects temperature has on, for
522 example, productivity and composition of the prey community (Hood et al., 2018; Nelson et
523 al., 2017; Yvon-Durocher, Montoya, Trimmer, & Woodward, 2011) and behavioural
524 interactions between the consumer and its prey and/or predators (Grigaltchik, Ward, &
525 Seebacher, 2012). Furthermore, non-thermal factors may restrict certain life stages to sub-
526 optimal habitats in the wild (e.g. predators restricting juveniles to refuges), further
527 complicating the mapping of environmental temperature to growth. Using the terminology of
528 Hutchinson (1957), controlled laboratory experiments (e.g. Peck et al. 2009, Messmer et al.
529 2017) estimate the growth axes of the *fundamental thermal niche*, whilst field studies like
530 ours estimate the growth axes of the *realised thermal niche* (Kearney, 2006). The mapping of
531 the fundamental thermal niche to the realised thermal niche is a function of both the intrinsic

532 and extrinsic effects of temperature, and the non-thermal constraints mentioned above (Holt,
533 2009).

534

535 Discordance between lab- and field-based estimates of the stage and temperature-dependence
536 of fish growth have been documented for Atlantic cod (Righton et al., 2010) and salmonids
537 (Jonsson & Jonsson, 2009). With respect to Murray cod, Svozil et al. (2018) determined the
538 effect of temperature on growth of larval Murray cod, but there have been no experiments on
539 the stage- and temperature-dependent growth of Murray cod beyond their first year of life.

540 We cannot, therefore, contrast our estimates of the growth axes of the Murray cod realised
541 thermal niche with those of their fundamental thermal niche. Numerous hypotheses could be
542 offered as to why the temperatures at which peak juvenile growth occurred were relatively
543 lower than anticipated (or, conversely, why the temperatures at which adult growth occurred
544 were relatively higher than anticipated). For example, Elliott and Hurley (2000) showed that
545 the optimal temperature for brown trout growth declines as food becomes scarce. With
546 respect to the present study, perhaps food for early juvenile Murray cod was in short supply,
547 depressing the temperature at which optimal growth occurred. In any case, research
548 programmes that meld multiple approaches to estimating both fundamental and realised
549 thermal niches are required to more confidently forecast the stage-dependent effects of
550 thermal change, and decipher the mechanisms underpinning patterns such as the TSR.

551

552 **4.2 Implications for management**

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

558

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

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

573

574 The challenge has three components, with the first of those components being more
575 surmountable than the others. First, river managers must build interannual heterogeneity into
576 water plans. Second, given adult Murray cod growth reaches a maximum when annual
577 discharge is also at its maximum, floods are likely a key component of the flow regime for
578 Murray cod. River managers, however, are often constrained to delivering flows that do not
579 exceed the bankfull threshold, to avoid damaging human infrastructure on floodplains (Bond
580 et al., 2014; Stoffels, Clarke, Rehwinkel, & McCarthy, 2013). Indeed, river regulation in the
581 MDB has greatly reduced the frequency and magnitude of floods (Sims, Chariton, Jin, &
582 Colloff, 2012) and by 2030 we may expect a further 13% decrease (cf. 2009) in total
583 discharge under a 'medium-severity' climate forecast (Kirby, Mainuddin, Ahmad, & Gao,
584 2013). Third, prolonged periods of low annual discharge will suppress cod growth,
585 highlighting the need for environmental flows during drought. Again, this will be a challenge
586 under the future MDB climate, which is forecast to experience more frequent and severe
587 droughts (CSIRO and Bureau of Meteorology, 2015).

588

589 As was the case for annual discharge, the effects of changes in annual temperature on Murray
590 cod growth were stage-specific, and generally robust to uncertainty generated by the
591 interaction annual temperature had with temporal stochasticity in discharge. The annual
592 temperature baseline for our four rivers is ca. 23.4 °C (baseline period: 1961-990, following
593 Intergovernmental Panel on Climate Change 2013; Appendix 2). According to the IPCC's
594 (2013) Representative Concentration Pathways (RCPs), by 2090, increases in mean air
595 temperatures within the MDB are forecast to be between 1.5 and 2.9 °C under RCP4.5 (low-
596 emission, 'best-case' scenario; stabilising CO₂ at 540 ppm by end of 21st century), and 2.9

597 and 5.3 °C under RCP8.5 ('business as usual' high-emission scenario; CO₂ reaching 940 ppm
598 by end of 21st century) (Ekström et al., 2015; Timbal et al., 2015; Watterson et al., 2015).
599 These forecasts imply that, by 2090, the mean maximum annual air temperatures of our study
600 systems will be between 24.9 °C and 28.7 °C. Other recent studies have highlighted the
601 potential for these scenarios to impact on native fish growth and distribution patterns within
602 the MDB (Galego de Oliveira et al., 2019; John R. Morrongiello et al., 2011; J. R.
603 Morrongiello et al., 2011). According to our data and model, growth rates of juvenile Murray
604 cod are optimal under IPCC baseline climatic conditions (23-24 °C), then decline as annual
605 temperature warms. If we assume stationarity of the Murray cod thermal niche, as well as the
606 temperature-dependence of all food web processes, then we can expect growth of juveniles to
607 decline under the IPCC RCP4.5 and RCP8.5 scenarios. Contrasting with juveniles, our model
608 and data indicate that growth rates of adults are below optimal under baseline climatic
609 conditions, and may increase as the climate warms under the RCP4.5 and RCP8.5 scenarios.
610
611 These divergent responses of life-stages to temperature generate considerable uncertainty as
612 to the effects of changing thermal regimes on the growth dynamics of Murray cod. In light of
613 this uncertainty and our observation that annual discharge has a stronger effect on Murray
614 cod growth than annual temperature, we suggest that the forecast reduction in the availability
615 of freshwater within the MDB (Sims et al. 2012, Kirby et al. 2013, Colloff et al. 2016)
616 presents a more immediate and greater climate-driven threat to Murray cod growth dynamics
617 than increases in annual mean temperature *per se*. This is not to say, however, that altered
618 thermal regimes pose less of a climate-driven challenge to resource managers than altered
619 river flows. Altered thermal regimes clearly present a great challenge to resource managers,
620 as demonstrated by recent mass fish mortality events associated with heat waves (Harris et al.
621 2018, Vertessy et al. 2019). Clearly, effects of climate change on both river flows and
622 thermal regimes will compound the long-standing threat to riverine populations posed by
623 damming and water abstraction. In light of this conclusion, an outstanding research challenge
624 is to integrate the effects of flow-temperature interactions on multiple population processes,
625 towards identification of pathways that are most threatening to population dynamics (e.g.
626 cessation of recruitment during prolonged low-flow periods) and, consequently, the
627 prioritisation of management interventions.

628

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635

636 **Data Availability Statement**

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

639

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1055 **TABLES**

1056 **Table 1.** Description of the three classes of Generalised Additive Mixed Models fitted to increment
 1057 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.

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1060 **Table 2.** Performance statistics for the models in the candidate set, sorted in increasing order by their1061 Akaike Information Criteria (AIC; decreasing log-likelihood ($\text{Log}(L)$)). $\Delta_i = \text{AIC}_i - \min(\text{AIC})$ is the1062 AIC model rank; and w_i is the Akaike weight of model i , interpreted as the approximate probability1063 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

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1067 **Table 3.** Parameter estimates of the final model of Murray cod growth. The first-order temporal1068 autocorrelation is given by ρ . NSE is the Nash-Sutcliffe Equilibrium; a measure of predictive

1069 accuracy on independent data. Effective degrees of freedom (edf) is an indicator of how curvilinear a

1070 smoother is (edf = 1 indicates a straight line, while edf > 8 indicates the smoother is highly non-

1071 linear).

$$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + f(F_{tij}, A_{tij}) + f(F_{tij}, T_{tij}, A_{tij}) + \varepsilon_{tij}$$

$$j = 1, \dots, n, \quad i = 1, \dots, n_j, \quad t = 1, \dots, n_{ij}$$

$$\alpha_j \sim N(0, \sigma_1^2), \quad \alpha_{ij} \sim N(0, \sigma_2^2), \quad \varepsilon_{ij} \sim N(0, \sigma^2)$$

$$\text{cor}(\varepsilon_s, \varepsilon_t) = \begin{cases} 1 & \text{if } s = t \\ \rho^{|t-s|} & \text{else} \end{cases}$$

$$R^2 = 0.82$$

$$\text{NSE} = 0.79$$

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

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1073 **FIGURE LEGENDS**

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1075 **Figure 1.** Magnitudes of the age-specific, combined effects of annual discharge and temperature on
1076 Murray cod growth. A smoother (+/- 95% CI) has been added to highlight the general change in effect
1077 size with age.

1078 **Figure 2.** Relative effect sizes of annual discharge and annual temperature on interannual dynamics of
1079 Murray cod growth. Predictions include fixed effects and the random effect of river system.
1080 Transparency of the columns was weighted by relative sample size within each river; the more
1081 transparent the smaller the sample size (see Appendix S1).

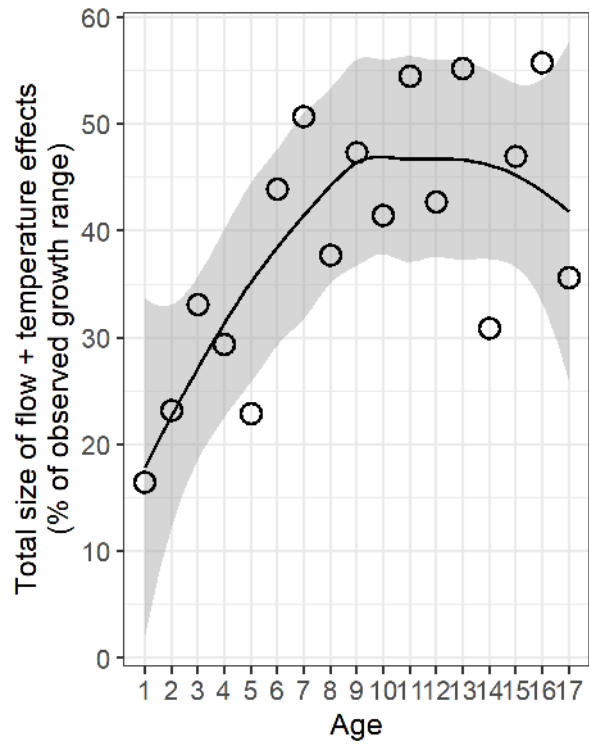
1082 **Figure 3.** Observed time series of annual temperature (a) and discharge (b) within the global domain
1083 of the training data set. Vertical dashed lines denote timing of major floods. Long-term mean
1084 discharge denoted by $y = 0$ in (b). The random effects of year (c; +/- 95% CI) and the fitted model (d;
1085 +/- 95% CI) are presented and model predictions beyond the temporal domain of river-specific data
1086 sets are also presented (where there is a line but no CI). Model fits/predictions are presented for 1+,
1087 5+ and 11+ individuals. Model fits include random effects of rivers, as well as the fixed, population
1088 effects.

1089 **Figure 4.** Stage-specific effects of annual discharge on the growth of Murray cod, incorporating
1090 uncertainty in those effects due to the interaction annual discharge has with interannual variability in
1091 annual temperature ('Temperature'; a form of environmental uncertainty), and environmental and
1092 statistical uncertainty ('Temperature + Statistical'). Annual discharge quantiles determined using the
1093 training data set.

1094 **Figure 5.** Stage-specific effects of annual temperature on the growth of Murray cod, incorporating
1095 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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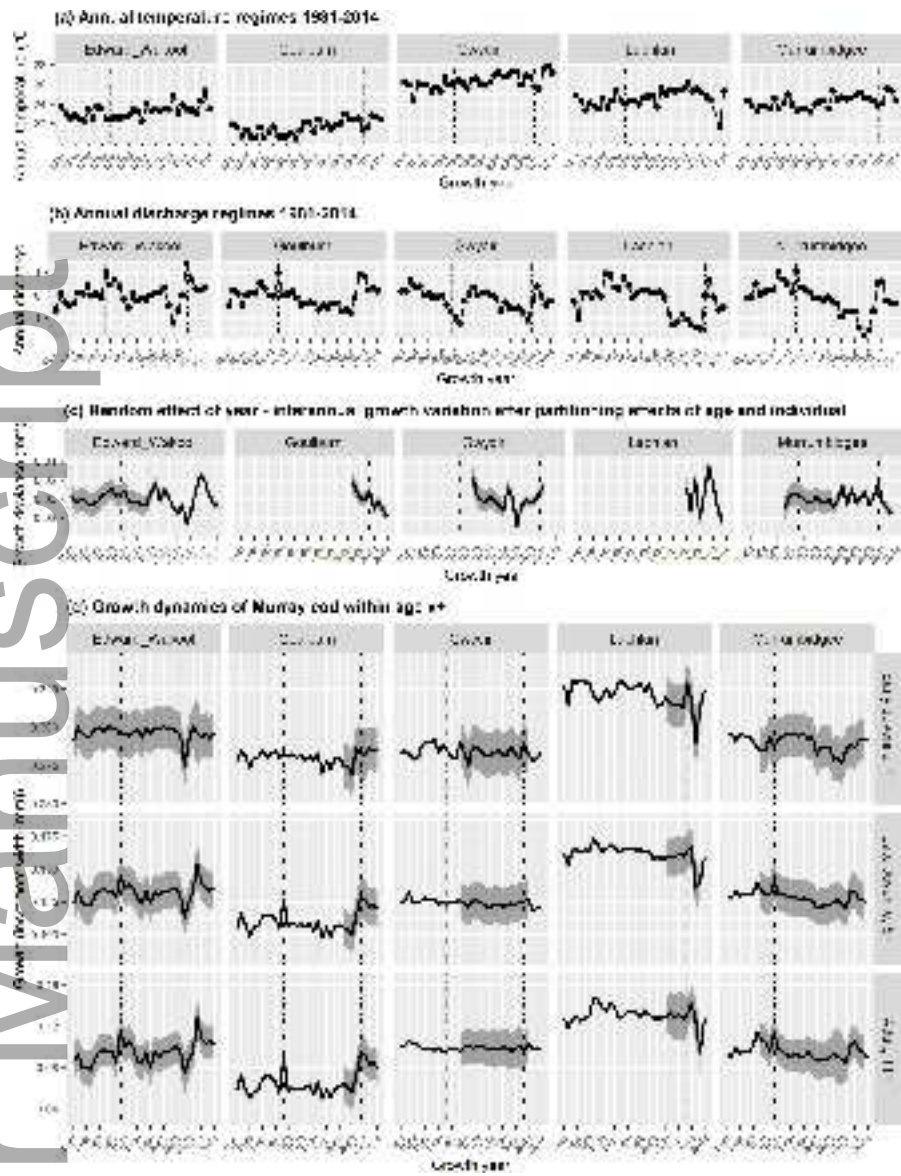


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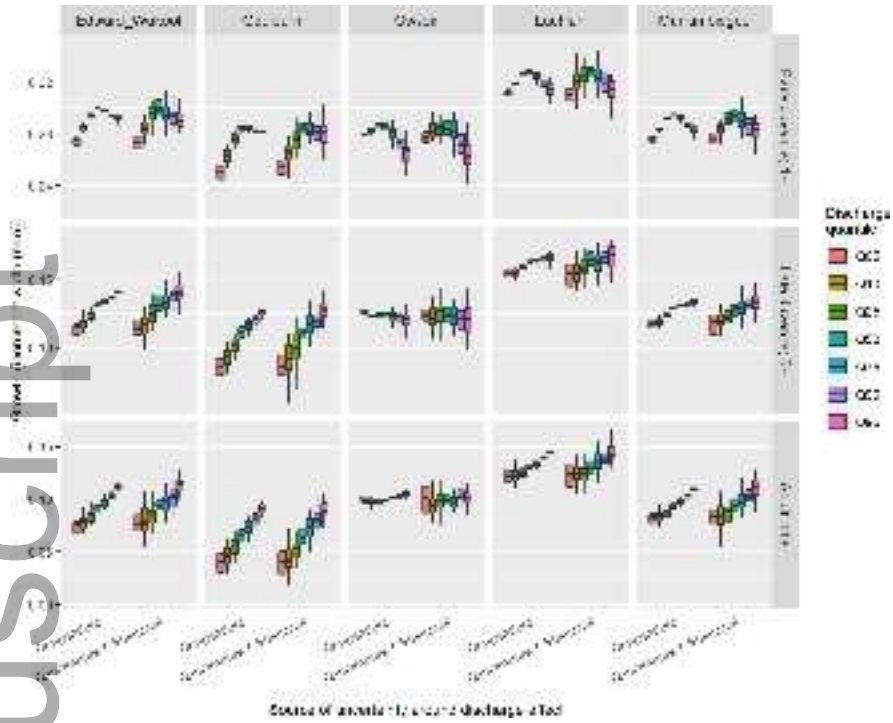


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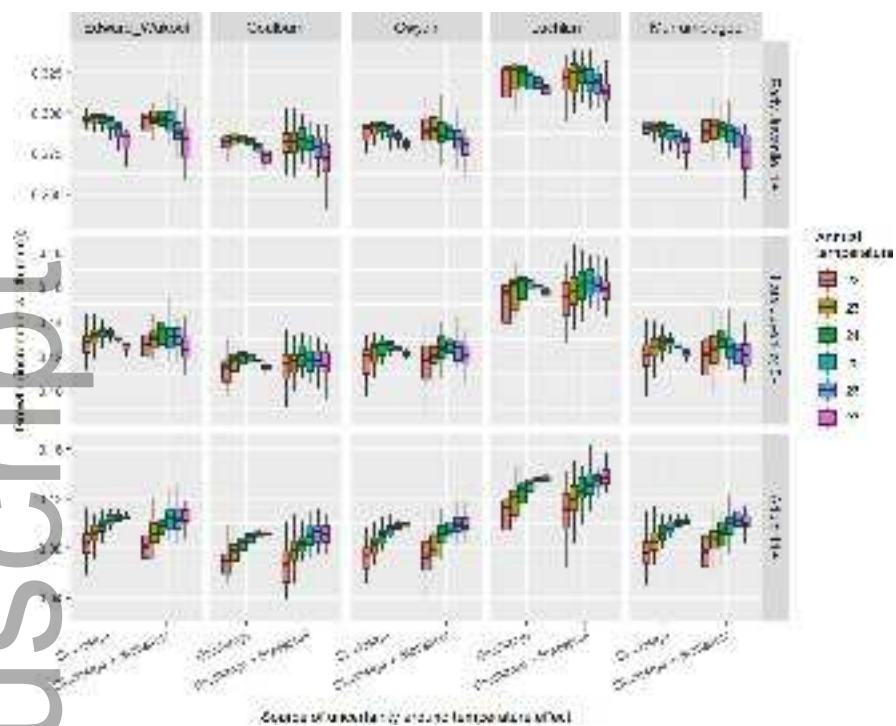
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