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

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12   Running title: Climate and river flow drive fish growth

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35

36

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 km^2, 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

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 $\geq$ 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

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).
415
416

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 CO_2 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; CO_2 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

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

640 **References**

641 Acreman, M., Arthington, A. H., Colloff, M. J., Couch, C., Crossman, N. D., Dyer, F., . . . Young, W.

642   (2014). Environmental flows for natural, hybrid, and novel riverine ecosystems in a changing

643   world. *Frontiers in Ecology and the Environment, 12*(8), 466-473. Retrieved from

644   https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/130134. doi:10.1890/130134

645 Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic

646   Control, 19*(6), 716-723. doi:10.1109/TAC.1974.1100705

647 Amundsen, P.-A., Bøhn, T., Popova, O. A., Staldvik, F. J., Reshetnikov, Y. S., Kashulin, N. A., & Lukin, A.

648   A. (2003). Ontogenetic niche shifts and resource partitioning in a subarctic piscivore fish

649   guild. *Hydrobiologia, 497*(1), 109-119. Retrieved from

650   https://doi.org/10.1023/A:1025465705717. doi:10.1023/a:1025465705717

651 Atkinson, D. (1994). Temperature and organism size: A biological law for ectotherms. In M. Begon &

652   A. H. Fitter (Eds.), *Advances in Ecological Research, Vol 25* (Vol. 25, pp. 1-58). London:

653   Academic Press Ltd-Elsevier Science Ltd.

654 Audzijonyte, A., Barneche, D. R., Baudron, A. R., Belmaker, J., Clark, T. D., Marshall, C. T., . . . van Rijn,

655   I. (2019). Is oxygen limitation in warming waters a valid mechanism to explain decreased

656   body sizes in aquatic ectotherms? *Global Ecology and Biogeography, 28*(2), 64-77. Retrieved

657   from https://onlinelibrary.wiley.com/doi/abs/10.1111/geb.12847. doi:10.1111/geb.12847

658 Audzijonyte, A., Kuparinen, A., Gorton, R., & Fulton, E. A. (2013). Ecological consequences of body

659   size decline in harvested fish species: positive feedback loops in trophic interactions amplify

660   human impact. *Biology Letters, 9*(2), 5. Retrieved from <Go to

661   ISI>://WOS:000331305400001. doi:10.1098/rsbl.2012.1103

662 Audzijonyte, A., Richards, S. A., Stuart-Smith, R. D., Pecl, G., Edgar, G. J., Barrett, N. S., . . . Blanchard,

663 J. L. (2020). Fish body sizes change with temperature but not all species shrink with warming.

664 *Nature Ecology & Evolution*, 11. Retrieved from <Go to ISI>://WOS:000523952600004.

665 doi:10.1038/s41559-020-1171-0

666 Balcombe, S. R., & Arthington, A. H. (2009). Temporal changes in fish abundance in response to

667 hydrological variability in a dryland floodplain river. *Marine and Freshwater Research, 60*(2),

668 146-159. Retrieved from https://www.publish.csiro.au/paper/MF08118.

669 doi:https://doi.org/10.1071/MF08118

670 Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., & Tara Marshall, C. (2014). Warming temperatures and

671 smaller body sizes: synchronous changes in growth of North Sea fishes. *Global Change*

672 *Biology, 20*(4), 1023-1031. Retrieved from

673 https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.12514. doi:10.1111/gcb.12514

674 Bayley, P. B. (1991). The flood pulse advantage and the restoration of river-floodplain systems.

675 *Regulated Rivers: Research & Management, 6*(2), 75-86. Retrieved from

676 https://onlinelibrary.wiley.com/doi/abs/10.1002/rrr.3450060203.

677 doi:10.1002/rrr.3450060203

678 Benke, A. C. (2001). Importance of flood regime to invertebrate habitat in an unregulated river–

679 floodplain ecosystem. *Journal of the North American Benthological Society, 20*(2), 225-240.

680 Retrieved from https://www.journals.uchicago.edu/doi/abs/10.2307/1468318.

681 doi:10.2307/1468318

682 Best, J. (2019). Anthropogenic stresses on the world's big rivers. *Nature Geoscience, 12*(1), 7-21.

683 Retrieved from <Go to ISI>://WOS:000454010200005. doi:10.1038/s41561-018-0262-x

684 Björnsson, B., & Steinarsson, A. (2002). The food-unlimited growth rate of Atlantic cod (Gadus

685 morhua). *Canadian Journal of Fisheries and Aquatic Sciences, 59*(3), 494-502. Retrieved from

686 https://doi.org/10.1139/f02-028. doi:10.1139/f02-028

687 Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S.

688 S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution.

689 *Trends in Ecology & Evolution, 24*(3), 127-135. Retrieved from

690 http://www.sciencedirect.com/science/article/pii/S0169534709000196.

691 doi:https://doi.org/10.1016/j.tree.2008.10.008

692 Bond, N., Costelloe, J., King, A., Warfe, D., Reich, P., & Balcombe, S. (2014). Ecological risks and

693 opportunities from engineered artificial flooding as a means of achieving environmental flow

694 objectives. *Frontiers in Ecology and the Environment, 12*(7), 386-394. Retrieved from

695 https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/130259. doi:10.1890/130259

696   Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow
697   regimes for aquatic biodiversity. *Environmental Management, 30*(4), 492-507. Retrieved
698   from <Go to ISI>://WOS:000177829800004. doi:10.1007/s00267-002-2737-0

699   Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical*
700   *Information-Theoretic Approach* (2nd ed.). New York: Springer.

701   Clark, M. S., Husmann, G., Thorne, M. A. S., Burns, G., Truebano, M., Peck, L. S., . . . Philipp, E. E. R.
702   (2013). Hypoxia impacts large adults first: consequences in a warming world. *Global Change*
703   *Biology, 19*(7), 2251-2263. Retrieved from
704   https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.12197. doi:10.1111/gcb.12197

705   CSIRO and Bureau of Meteorology. (2015). *Climate Change in Australia Information for Australia's*
706   *Natural Resource Management Regions: Technical Report*. Retrieved from

707   Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in aquatic
708   ecosystems. *Proceedings of the National Academy of Sciences, 106*(31), 12788-12793.
709   Retrieved from https://www.pnas.org/content/pnas/106/31/12788.full.pdf.
710   doi:10.1073/pnas.0902080106

711   Davidson, R. S., Letcher, B. H., & Nislow, K. H. (2010). Drivers of growth variation in juvenile Atlantic
712   salmon (Salmo salar): an elasticity analysis approach. *Journal of Animal Ecology, 79*(5), 1113-
713   1121. Retrieved from https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-
714   2656.2010.01708.x. doi:10.1111/j.1365-2656.2010.01708.x

715   de Roos, A., & Persson, L. (2013). *Population and Community Ecology of Ontogenetic Development*.
716   Princeton, New Jersey: Princeton University Press.

717   Duston, J., Astatkie, T., & MacIssac, P. F. (2004). Effect of body size on growth and food conversion of
718   juvenile striped bass reared at 16-28 degrees C in freshwater and seawater. *Aquaculture,*
719   *234*(1-4), 589-600. Retrieved from <Go to ISI>://WOS:000221069000038.
720   doi:10.1016/j.aquaculture.2004.01.005

721   Ebner, B. (2006). Murray cod an apex predator in the Murray River, Australia. *Ecology of Freshwater*
722   *Fish, 15*(4), 510-520. Retrieved from
723   https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1600-0633.2006.00191.x.
724   doi:10.1111/j.1600-0633.2006.00191.x

725   Ekström, M., Abbs, D., Bhend, J., Chiew, F., Kirono, D., Lucas, C., . . . Whetton, P. (Eds.). (2015).
726   *Central Slopes Cluster Report*. Australia: CSIRO and Bureau of Meteorology.

727   Elliott, J. M., & Hurley, M. A. (2000). Optimum energy intake and gross efficiency of energy
728   conversion for brown trout, Salmo trutta, feeding on invertebrates or fish. *Freshwater*

729   *Biology, 44*(4), 605-615. Retrieved from <Go to ISI>://WOS:000089193400004.

730   doi:10.1046/j.1365-2427.2000.00605.x

731 Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., . . . Wardle, D. A.

732   (2011). Trophic Downgrading of Planet Earth. *Science, 333*(6040), 301-306. Retrieved from

733   <Go to ISI>://WOS:000292732000031. doi:10.1126/science.1205106

734 Fausch, K. D., Torgersen, C. E., Baxter, C. V., & Li, H. W. (2002). Landscapes to Riverscapes: Bridging

735   the Gap between Research and Conservation of Stream Fishes: A Continuous View of the

736   River is Needed to Understand How Processes Interacting among Scales Set the Context for

737   Stream Fishes and Their Habitat. *Bioscience, 52*(6), 483-498. Retrieved from

738   https://doi.org/10.1641/0006-3568(2002)052[0483:LTRBTG]2.0.CO;2. doi:10.1641/0006-

739   3568(2002)052[0483:Ltrbtg]2.0.Co;2

740 Galego de Oliveira, A., Bailly, D., Cassemiro, F. A. S., Couto, E. V. d., Bond, N., Gilligan, D., . . .

741   Kennard, M. J. (2019). Coupling environment and physiology to predict effects of climate

742   change on the taxonomic and functional diversity of fish assemblages in the Murray-Darling

743   Basin, Australia. *Plos One, 14*(11), e0225128. Retrieved from

744   https://doi.org/10.1371/journal.pone.0225128. doi:10.1371/journal.pone.0225128

745 Gelman, A., & Hill, J. (2007). *Data Analysis Using Regression and Multilevel/Hierarchical Models*. New

746   York, America: Cambridge University Press.

747 Grigaltchik, V. S., Ward, A. J. W., & Seebacher, F. (2012). Thermal acclimation of interactions:

748   differential responses to temperature change alter predator-prey relationships. *Proceedings

749   of the Royal Society B: Biological Sciences, 279*(1744), 4058-4064. Retrieved from

750   https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2012.1277

751   doi:doi:10.1098/rspb.2012.1277

752 Hastie, T., Tibshirani, R., & Friedman, J. H. (2009). *The Elements of Statistical Learning: Data Mining,

753   Inference and Prediction* (2nd ed.). New York: Springer.

754 He, F., Zarfl, C., Bremerich, V., David, J. N. W., Hogan, Z., Kalinkat, G., . . . Jähnig, S. C. (2019). The

755   global decline of freshwater megafauna. *Global Change Biology, 25*(11), 3883-3892.

756   Retrieved from https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.14753.

757   doi:10.1111/gcb.14753

758 Holt, R. D. (2009). Bringing the Hutchinsonian niche into the 21st century: Ecological and

759   evolutionary perspectives. *Proceedings of the National Academy of Sciences,

760   106*(Supplement 2), 19659-19665. Retrieved from

761   https://www.pnas.org/content/pnas/106/Supplement_2/19659.full.pdf.

762   doi:10.1073/pnas.0905137106

763 Hood, J. M., Benstead, J. P., Cross, W. F., Huryn, A. D., Johnson, P. W., Gislason, G. M., . . . Tran, C.
764   (2018). Increased resource use efficiency amplifies positive response of aquatic primary
765   production to experimental warming. *Global Change Biology, 24*(3), 1069-1084. Retrieved
766   from <Go to ISI>://WOS:000425396700018. doi:10.1111/gcb.13912

767 Horne, C. R., Hirst, A. G., & Atkinson, D. (2017). Seasonal body size reductions with warming covary
768   with major body size gradients in arthropod species. *Proceedings of the Royal Society B:*
769   *Biological Sciences, 284*(1851), 20170238. Retrieved from
770   https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2017.0238.
771   doi:doi:10.1098/rspb.2017.0238

772 Humphries, P., King, A. J., McCasker, N., Kopf, R. K., Stoffels, R., Zampatti, B. P., & Price, A. E. (2020).
773   Riverscape recruitment: a conceptual synthesis of drivers of fish recruitment in rivers.
774   *Canadian Journal of Fisheries and Aquatic Sciences, 77*(2), 213-225. Retrieved from
775   https://doi.org/10.1139/cjfas-2018-0138. doi:10.1139/cjfas-2018-0138

776 Huss, M., Lindmark, M., Jacobson, P., van Dorst, R. M., & Gårdmark, A. (2019). Experimental
777   evidence of gradual size-dependent shifts in body size and growth of fish in response to
778   warming. *Global Change Biology, 25*(7), 2285-2295. Retrieved from
779   https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.14637. doi:10.1111/gcb.14637

780 Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology,*
781   *22*, 415–427.

782 IPCC. (2013). Climate Change 2013: The Physical Science Basis. In *Contribution of Working Group I to*
783   *the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge,
784   UK, and New York, NY, USA: Cambridge University Press.

785 Izzo, C., Doubleday, Z. A., Grammer, G. L., Barnes, T. C., Delean, S., Ferguson, G. J., . . . Gillanders, B.
786   M. (2016). Multi-species response to rapid environmental change in a large estuary system:
787   A biochronological approach. *Ecological Indicators, 69*, 739-748. Retrieved from <Go to
788   ISI>://WOS:000388785100072. doi:10.1016/j.ecolind.2016.05.019

789 Jensen, A. J., & Johnsen, B. O. (1999). The functional relationship between peak spring floods and
790   survival and growth of juvenile Atlantic Salmon (Salmo salar) and Brown Trout (Salmo
791   trutta). *Functional Ecology, 13*(6), 778-785. Retrieved from <Go to
792   ISI>://WOS:000084788600006. doi:10.1046/j.1365-2435.1999.00358.x

793 Jobling, M. (1996). Temperature and growth: modulation of growth rate via temperature change. In
794   C. M. Wood & D. G. McDonald (Eds.), *Global Warming: Implications for Freshwater and*
795   *Marine Fish* (pp. 225-253). Cambridge, United Kingdom: Cambridge University Press.

796 Jonsson, B., & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous
797   Atlantic salmon Salmo salar and brown trout Salmo trutta, with particular reference to water
798   temperature and flow. *Journal of Fish Biology, 75*(10), 2381-2447. Retrieved from <Go to
799   ISI>://WOS:000273899600001. doi:10.1111/j.1095-8649.2009.02380.x

800 Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems.
801   In D. P. Dodge (Ed.), *Proceedings of the International Large River Symposium* (Vol. 106, pp.
802   110-127): Canadian Special Publications in Fisheries and Aquatic Sciences.

803 Kearney, M. (2006). Habitat, environment and niche: what are we modelling? *Oikos, 115*(1), 186-
804   191. Retrieved from https://onlinelibrary.wiley.com/doi/abs/10.1111/j.2006.0030-
805   1299.14908.x. doi:10.1111/j.2006.0030-1299.14908.x

806 Kingsolver, J. G. (2009). The Well-Temperatured Biologist. *American Naturalist, 174*(6), 755-768.
807   Retrieved from <Go to ISI>://WOS:000271425900004. doi:10.1086/648310

808 Kingsolver, J. G., & Huey, R. B. (2008). Size, temperature, and fitness: three rules. *Evolutionary*
809   *Ecology Research, 10*(2), 251-268. Retrieved from <Go to ISI>://WOS:000256465000007.

810 Kirby, J. M., Mainuddin, M., Ahmad, M. D., & Gao, L. (2013). Simplified Monthly Hydrology and
811   Irrigation Water Use Model to Explore Sustainable Water Management Options in the
812   Murray-Darling Basin. *Water Resources Management, 27*(11), 4083-4097. Retrieved from
813   https://doi.org/10.1007/s11269-013-0397-x. doi:10.1007/s11269-013-0397-x

814 Koehn, J. D., McKenzie, J. A., O'Mahony, D. J., Nicol, S. J., O'Connor, J. P., & O'Connor, W. G. (2009).
815   Movements of Murray cod (Maccullochella peelii peelii) in a large Australian lowland river.
816   *Ecology of Freshwater Fish, 18*(4), 594-602. Retrieved from <Go to
817   ISI>://WOS:000271631000011. doi:10.1111/j.1600-0633.2009.00375.x

818 Koehn, J. D., & Nicol, S. J. (2014). Comparative habitat use by large riverine fishes. *Marine and*
819   *Freshwater Research, 65*(2), 164-174. Retrieved from <Go to ISI>://WOS:000331383000008.
820   doi:10.1071/mf13011

821 Leigh, S. J., & Zampatti, B. P. (2013). Movement and mortality of Murray cod, Maccullochella peelii,
822   during overbank flows in the lower River Murray, Australia. *Australian Journal of Zoology,*
823   *61*(2), 160-169. Retrieved from <Go to ISI>://WOS:000321628400007. doi:10.1071/zo12124

824 Lindmark, M., Huss, M., Ohlberger, J., & Gårdmark, A. (2018). Temperature-dependent body size
825   effects determine population responses to climate warming. *Ecology Letters, 21*(2), 181-189.
826   Retrieved from https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.12880.
827   doi:10.1111/ele.12880

828 Lintermans, M. (2007). *Fishes of the Murray-Darling Basin: An Introductory Guide*. Canberra, ACT:
829   Murray-Darling Basin Commission.

830   Lytle, D. A., & Poff, N. L. (2004). Adaptation to natural flow regimes. *Trends in Ecology & Evolution,*

831   *19*(2), 94-100. Retrieved from <Go to ISI>://WOS:000188931400010.

832   doi:10.1016/j.tree.2003.10.002

833   McInerney, P. J., Stoffels, R. J., Shackleton, M. E., & Davey, C. D. (2017). Flooding drives a

834   macroinvertebrate biomass boom in ephemeral floodplain wetlands. *Freshwater Science,*

835   *36*(4), 726-738. Retrieved from

836   https://www.journals.uchicago.edu/doi/abs/10.1086/694905. doi:10.1086/694905

837   Messmer, V., Pratchett, M. S., Hoey, A. S., Tobin, A. J., Coker, D. J., Cooke, S. J., & Clark, T. D. (2017).

838   Global warming may disproportionately affect larger adults in a predatory coral reef fish.

839   *Global Change Biology, 23*(6), 2230-2240. Retrieved from

840   https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.13552. doi:10.1111/gcb.13552

841   Mohseni, O., Stefan, H. G., & Erickson, T. R. (1998). A nonlinear regression model for weekly stream

842   temperatures. *Water Resources Research, 34*(10), 2685-2692. Retrieved from

843   https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/98WR01877.

844   doi:10.1029/98wr01877

845   Morita, K., Fukuwaka, M., Tanimata, N., & Yamamura, O. (2010). Size-dependent thermal

846   preferences in a pelagic fish. *Oikos, 119*(8), 1265-1272. Retrieved from <Go to

847   ISI>://WOS:000280356200007. doi:10.1111/j.1600-0706.2009.18125.x

848   Morrongiello, J. R., Beatty, S. J., Bennett, J. C., Crook, D. A., Ikedife, D. N. E. N., Kennard, M. J., . . .

849   Rayner, T. (2011). Climate change and its implications for Australia's freshwater fish. *Marine*

850   *and Freshwater Research, 62*(9), 1082-1098. Retrieved from

851   https://www.publish.csiro.au/paper/MF10308. doi:https://doi.org/10.1071/MF10308

852   Morrongiello, J. R., Crook, D. A., King, A. J., Ramsey, D. S. L., & Brown, P. (2011). Impacts of drought

853   and predicted effects of climate change on fish growth in temperate Australian lakes. *Global*

854   *Change Biology, 17*(2), 745-755. Retrieved from <Go to ISI>://WOS:000285878000009.

855   doi:10.1111/j.1365-2486.2010.02259.x

856   Morrongiello, J. R., & Thresher, R. E. (2015). A statistical framework to explore ontogenetic growth

857   variation among individuals and populations: a marine fish example. *Ecological Monographs,*

858   *85*(1), 93-115. Retrieved from <Go to ISI>://WOS:000349389800006. doi:10.1890/13-2355.1

859   Morrongiello, J. R., Walsh, C. T., Gray, C. A., Stocks, J. R., & Crook, D. A. (2014). Environmental

860   change drives long-term recruitment and growth variation in an estuarine fish. *Global*

861   *Change Biology, 20*(6), 1844-1860. Retrieved from <Go to ISI>://WOS:000336482700013.

862   doi:10.1111/gcb.12545

863 Nash, J. E., & Sutcliffe, J. V. (1970). River flow forecasting through conceptual models part I — A

864   discussion of principles. *Journal of Hydrology, 10*(3), 282-290. Retrieved from

865   http://www.sciencedirect.com/science/article/pii/0022169470902556.

866   doi:https://doi.org/10.1016/0022-1694(70)90255-6

867 Nelson, D., Benstead, J. P., Huryn, A. D., Cross, W. F., Hood, J. M., Johnson, P. W., . . . Ólafsson, J. S.

868   (2017). Experimental whole-stream warming alters community size structure. *Global Change*

869   *Biology, 23*(7), 2618-2628. Retrieved from

870   https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.13574. doi:10.1111/gcb.13574

871 Ning, N. S. P., Nielsen, D. L., Paul, W. L., Hillman, T. J., & Suter, P. J. (2010). Microinvertebrate

872   dynamics in riverine slackwater and mid-channel habitats in relation to physico-chemical

873   parameters and food availability. *River Research and Applications, 26*(3), 279-296. Retrieved

874   from https://onlinelibrary.wiley.com/doi/abs/10.1002/rra.1266. doi:10.1002/rra.1266

875 Nislow, K. H., Sepulveda, A. J., & Folt, C. L. (2004). Mechanistic Linkage of Hydrologic Regime to

876   Summer Growth of Age-0 Atlantic Salmon. *Transactions of the American Fisheries Society,*

877   *133*(1), 79-88. Retrieved from https://doi.org/10.1577/T02-168. doi:10.1577/T02-168

878 Nunn, A. D., Cowx, I. G., Frear, P. A., & Harvey, J. P. (2003). Is water temperature an adequate

879   predictor of recruitment success in cyprinid fish populations in lowland rivers? *Freshwater*

880   *Biology, 48*(4), 579-588. Retrieved from

881   https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1365-2427.2003.01033.x.

882   doi:10.1046/j.1365-2427.2003.01033.x

883 Nunn, A. D., Harvey, J. P., Britton, J. R., Frear, P. A., & Cowx, I. G. (2007). Fish, climate and the Gulf

884   Stream: the influence of abiotic factors on the recruitment success of cyprinid fishes in

885   lowland rivers. *Freshwater Biology, 52*(8), 1576-1586. Retrieved from <Go to

886   ISI>://WOS:000247905900014. doi:10.1111/j.1365-2427.2007.01789.x

887 Ohlberger, J. (2013). Climate warming and ectotherm body size – from individual physiology to

888   community ecology. *Functional Ecology, 27*(4), 991-1001. Retrieved from

889   https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2435.12098.

890   doi:10.1111/1365-2435.12098

891 Olden, J. D., & Naiman, R. J. (2010). Incorporating thermal regimes into environmental flows

892   assessments: modifying dam operations to restore freshwater ecosystem integrity.

893   *Freshwater Biology, 55*(1), 86-107. Retrieved from <Go to ISI>://WOS:000272836500006.

894   doi:10.1111/j.1365-2427.2009.02179.x

895 Olsen, L. R. (2017). groupdata2: Creating Groups from Data. R package version 1.0.0.

896   https://CRAN.R-project.org/package=groupdata2.

897 Peck, L. S., Clark, M. S., Morley, S. A., Massey, A., & Rossetti, H. (2009). Animal temperature limits

898   and ecological relevance: effects of size, activity and rates of change. *Functional Ecology,*

899   *23*(2), 248-256. Retrieved from

900   https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2435.2008.01537.x.

901   doi:10.1111/j.1365-2435.2008.01537.x

902 Peck, L. S., Souster, T., & Clark, M. S. (2013). Juveniles Are More Resistant to Warming than Adults in

903   4 Species of Antarctic Marine Invertebrates. *Plos One, 8*(6), e66033. Retrieved from

904   https://doi.org/10.1371/journal.pone.0066033. doi:10.1371/journal.pone.0066033

905 Pinheiro, J. C., & Bates, D. M. (2000). *Mixed-effects models in S and S-Plus*. New York, NY: Springer

906   Verlag New York LLC.

907 Poff, N. L. (2018). Beyond the natural flow regime? Broadening the hydro-ecological foundation to

908   meet environmental flows challenges in a non-stationary world. *Freshwater Biology, 63*(8),

909   1011-1021. Retrieved from https://onlinelibrary.wiley.com/doi/abs/10.1111/fwb.13038.

910   doi:10.1111/fwb.13038

911 Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., . . . Stromberg, J. C.

912   (1997). The natural flow regime. *Bioscience, 47*(11), 769-784. Retrieved from <Go to

913   ISI>://WOS:A1997YH05400012. doi:10.2307/1313099

914 Policansky, D. (2015). Size, Age and Demography of Metamorphosis and Sexual Maturation in Fishes.

915   *American Zoologist, 23*(1), 57-63. Retrieved from https://doi.org/10.1093/icb/23.1.57.

916   doi:10.1093/icb/23.1.57

917 Price, A. E., Humphries, P., Gawne, B., & Thoms, M. C. (2012). Effects of discharge regulation on

918   slackwater characteristics at multiple scales in a lowland river. *Canadian Journal of Fisheries*

919   *and Aquatic Sciences, 70*(2), 253-262. Retrieved from https://doi.org/10.1139/cjfas-2012-

920   0164. doi:10.1139/cjfas-2012-0164

921 Righton, D. A., Andersen, K. H., Neat, F., Thorsteinsson, V., Steingrund, P., Svedang, H., . . . Metcalfe,

922   J. (2010). Thermal niche of Atlantic cod Gadus morhua: limits, tolerance and optima. *Marine*

923   *Ecology Progress Series, 420*, 1-U344. Retrieved from <Go to ISI>://WOS:000285419300001.

924   doi:10.3354/meps08889

925 Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., . . . Wirsing, A.

926   J. (2014). Status and Ecological Effects of the World's Largest Carnivores. *Science, 343*(6167),

927   1241484. Retrieved from

928   https://science.sciencemag.org/content/sci/343/6167/1241484.full.pdf.

929   doi:10.1126/science.1241484

930   Seneviratne, S. I., Donat, M. G., Mueller, B., & Alexander, L. V. (2014). No pause in the increase of

931   hot temperature extremes. *Nature Climate Change, 4*(3), 161-163. Retrieved from <Go to

932   ISI>://WOS:000333669100008. doi:10.1038/nclimate2145

933   Sims, N. C., Chariton, A. A., Jin, H. D., & Colloff, M. J. (2012). A Classification of Floodplains and

934   Wetlands of the Murray-Darling Basin Based on Changes in Flows Following Water Resource

935   Development. *Wetlands, 32*(2), 239-248. Retrieved from <Go to

936   ISI>://WOS:000302031800005. doi:10.1007/s13157-011-0231-2

937   Sinclair, B. J., Marshall, K. E., Sewell, M. A., Levesque, D. L., Willett, C. S., Slotsbo, S., . . . Huey, R. B.

938   (2016). Can we predict ectotherm responses to climate change using thermal performance

939   curves and body temperatures? *Ecology Letters, 19*(11), 1372-1385. Retrieved from <Go to

940   ISI>://WOS:000386228300008. doi:10.1111/ele.12686

941   Spurgeon, J. J., & Pegg, M. A. (2017). Juvenile growth of a macrohabitat generalist tied to

942   hydrological character of large-river system. *Freshwater Biology, 62*(2), 291-302. Retrieved

943   from <Go to ISI>://WOS:000393793100006. doi:10.1111/fwb.12867

944   Stoffels, R. J. (2013). Trophic Ecology. In P. Humphries & K. F. Walker (Eds.), *Ecology of Australian*

945   *Freshwater Fishes* (pp. 131-158). VIC, Australia: CSIRO Publishing.

946   Stoffels, R. J., Bond, N. R., & Nicol, S. (2018). Science to support the management of riverine flows.

947   *Freshwater Biology, 63*(8), 996-1010. Retrieved from

948   https://onlinelibrary.wiley.com/doi/abs/10.1111/fwb.13061. doi:10.1111/fwb.13061

949   Stoffels, R. J., Clarke, K. R., Rehwinkel, R. A., & McCarthy, B. J. (2013). Response of a floodplain fish

950   community to river-floodplain connectivity: natural versus managed reconnection. *Canadian*

951   *Journal of Fisheries and Aquatic Sciences, 71*(2), 236-245. Retrieved from

952   https://doi.org/10.1139/cjfas-2013-0042. doi:10.1139/cjfas-2013-0042

953   Svozil, D. P., Kopf, R. K., Watts, R. J., & Nicholls, A. O. (2018). Temperature-dependent larval survival

954   and growth differences among populations of Murray cod (<i>Maccullochella peelii</i>).

955   *Marine and Freshwater Research*, -. Retrieved from

956   https://www.publish.csiro.au/paper/MF18178. doi:https://doi.org/10.1071/MF18178

957   Tanaka, Y., Satoh, K., Iwahashi, M., & Yamada, H. (2006). Growth-dependent recruitment of Pacific

958   bluefin tuna Thunnus orientalis in the northwestern Pacific Ocean. *Marine Ecology Progress*

959   *Series, 319*, 225-235. Retrieved from <Go to ISI>://WOS:000241102600020.

960   doi:10.3354/meps319225

961   Thiem, J. D., Wooden, I. J., Baumgartner, L. J., Butler, G. L., Forbes, J., Taylor, M. D., & Watts, R. J.

962   (2018). Abiotic drivers of activity in a large, freeranging, freshwater teleost, Murray cod

963   (Maccullochella peelii). *Plos One, 13*(6), 14. Retrieved from <Go to

964   ISI>://WOS:000434728100044. doi:10.1371/journal.pone.0198972

965 Timbal, B., Abbs, D., Bhend, J., Chiew, F., Church, J., Ekström, M., . . . Whetton, P. (Eds.). (2015).

966   *Murray Basin Cluster Report*. Australia: CSIRO and Bureau of Meteorology.

967 Tonkin, J. D., Poff, N. L., Bond, N. R., Horne, A., Merritt, D. M., Reynolds, L. V., . . . Lytle, D. A. (2019).

968   Prepare river ecosystems for an uncertain future. *Nature, 570*(7761), 301-303. Retrieved

969   from <Go to ISI>://WOS:000472145700042. doi:10.1038/d41586-019-01877-1

970 Tonkin, Z., Kitchingman, A., Lyon, J., Kearns, J., Hackett, G., O'Mahony, J., . . . Bird, T. (2017). Flow

971   magnitude and variability influence growth of two freshwater fish species in a large

972   regulated floodplain river. *Hydrobiologia, 797*(1), 289-301. Retrieved from <Go to

973   ISI>://WOS:000404174200021. doi:10.1007/s10750-017-3192-5

974 Tonkin, Z. D., King, A. J., Robertson, A. I., & Ramsey, D. S. L. (2011). Early fish growth varies in

975   response to components of the flow regime in a temperate floodplain river. *Freshwater

976   Biology, 56*(9), 1769-1782. Retrieved from <Go to ISI>://WOS:000293523200006.

977   doi:10.1111/j.1365-2427.2011.02612.x

978 van Dijk, A. I. J. M., Beck, H. E., Crosbie, R. S., de Jeu, R. A. M., Liu, Y. Y., Podger, G. M., . . . Viney, N.

979   R. (2013). The Millennium Drought in southeast Australia (2001–2009): Natural and human

980   causes and implications for water resources, ecosystems, economy, and society. *Water

981   Resources Research, 49*(2), 1040-1057. Retrieved from

982   https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1002/wrcr.20123.

983   doi:10.1002/wrcr.20123

984 van Rijn, I., Buba, Y., DeLong, J., Kiflawi, M., & Belmaker, J. (2017). Large but uneven reduction in fish

985   size across species in relation to changing sea temperatures. *Global Change Biology, 23*(9),

986   3667-3674. Retrieved from https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.13688.

987   doi:10.1111/gcb.13688

988 van Vliet, M. T. H., Ludwig, F., & Kabat, P. (2013). Global streamflow and thermal habitats of

989   freshwater fishes under climate change. *Climatic Change, 121*(4), 739-754. Retrieved from

990   <Go to ISI>://WOS:000327395700013. doi:10.1007/s10584-013-0976-0

991 van Vliet, M. T. H., Ludwig, F., Zwolsman, J. J. G., Weedon, G. P., & Kabat, P. (2011). Global river

992   temperatures and sensitivity to atmospheric warming and changes in river flow. *Water

993   Resources Research, 47*, 19. Retrieved from <Go to ISI>://WOS:000287819300002.

994   doi:10.1029/2010wr009198

995 Vietz, G. J., Sammonds, M. J., & Stewardson, M. J. (2013). Impacts of flow regulation on slackwaters

996   in river channels. *Water Resources Research, 49*(4), 1797-1811. Retrieved from

997   https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1002/wrcr.20094.

998   doi:10.1002/wrcr.20094

999   Vincenzi, S., Satterthwaite, W. H., & Mangel, M. (2012). Spatial and temporal scale of density-

1000   dependent body growth and its implications for recruitment, population dynamics and

1001   management of stream-dwelling salmonid populations. *Reviews in Fish Biology and*

1002   *Fisheries, 22*(3), 813-825. Retrieved from <Go to ISI>://WOS:000307505000018.

1003   doi:10.1007/s11160-011-9247-1

1004   Vorosmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., . . . Davies, P.

1005   M. (2010). Global threats to human water security and river biodiversity. *Nature, 467*(7315),

1006   555-561. Retrieved from <Go to ISI>://WOS:000282273100031. doi:10.1038/nature09440

1007   Wackerly, D. D., Mendenhall, W., & Scheaffer, R. L. (2002). *Mathematical Statistics with Applications*

1008   (6th ed.): Wadsworth Group.

1009   Wainwright, P. C., & Richard, B. A. (1995). Predicting patterns of prey use from morphology of fishes.

1010   *Environmental Biology of Fishes, 44*(1), 97-113. Retrieved from

1011   https://doi.org/10.1007/BF00005909. doi:10.1007/bf00005909

1012   Wang, W., & Gelman, A. (2015). Difficulty of selecting among multilevel models using predictive

1013   accuracy. *Statistics and Its Interface, 8*(2), 153-160. Retrieved from <Go to

1014   ISI>://WOS:000353052100004. doi:10.4310/SII.2015.v8.n2.a3

1015   Watterson, I., Abbs, D., Bhend, J., Chiew, F., Church, J., Ekström, M., . . . Whetton, P. (Eds.). (2015).

1016   *Rangelands Cluster Report*. Australia: CSIRO and Bureau of Meteorology.

1017   Webb, B. W., Clack, P. D., & Walling, D. E. (2003). Water–air temperature relationships in a Devon

1018   river system and the role of flow. *Hydrological Processes, 17*(15), 3069-3084. Retrieved from

1019   https://onlinelibrary.wiley.com/doi/abs/10.1002/hyp.1280. doi:10.1002/hyp.1280

1020   Werner, E. E., & Gilliam, J. F. (1984). The Ontogenetic Niche and Species Interactions in Size-

1021   Structured Populations. *Annual Review of Ecology and Systematics, 15*(1), 393-425.

1022   Retrieved from

1023   https://www.annualreviews.org/doi/abs/10.1146/annurev.es.15.110184.002141.

1024   doi:10.1146/annurev.es.15.110184.002141

1025   Winemiller, K. O. (1989). Ontogenetic diet shifts and resource partitioning among piscivorous fishes

1026   in the Venezuelan ilanos. *Environmental Biology of Fishes, 26*(3), 177-199. Retrieved from

1027   https://doi.org/10.1007/BF00004815. doi:10.1007/bf00004815

1028   Winemiller, K. O. (2004). Floodplain River Food webs: Generalisations and Implications for Fisheries

1029   Management. In W. R. & T. Petr (Eds.), *Proceedings of the Second International Symposium*

1030 *on the Management of Large Rivers for Fisheries* (Vol. 1, pp. 285-309). Bangkok, Thailand:

1031 FAO Regional Office for Asia and the Pacific, RAP Publication 2004/16.

1032 Wood, S., & Scheipl, F. (2017). gamm4: Generalised Additive Mixed Models using mgcv and lme4. R

1033 package version 0.2-5.

1034 Wood, S. N. (2017). *Generalised Additive Models: An Introduction with R* (Second ed.). Boca Raton,

1035 FL: Chapman and Hall/CRCTexts In Statistical Science.

1036 Wootton, R. J. (2011). Growth: Environmental Effects. In A. P. Farrell (Ed.), *Encyclopedia of Fish*

1037 *Physiology* (pp. 1629-1635). San Diego: Academic Press.

1038 Wu, H., Kimball, J. S., Elsner, M. M., Mantua, N., Adler, R. F., & Stanford, J. (2012). Projected climate

1039 change impacts on the hydrology and temperature of Pacific Northwest rivers. *Water*

1040 *Resources Research, 48*, 23. Retrieved from <Go to ISI>://WOS:000311850700001.

1041 doi:10.1029/2012wr012082

1042 Yvon-Durocher, G., Montoya, J. M., Trimmer, M., & Woodward, G. (2011). Warming alters the size

1043 spectrum and shifts the distribution of biomass in freshwater ecosystems. *Global Change*

1044 *Biology, 17*(4), 1681-1694. Retrieved from

1045 https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.2010.02321.x.

1046 doi:10.1111/j.1365-2486.2010.02321.x

1047 Zuur, A., Ieno, E. N., Walker, N., Savaliev, A. A., & M., S. G. (2009). *Mixed Effects Models and*

1048 *Extensions in Ecology with R*. New York, USA: Springer.

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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
Spatial, intrinsic and year effects		
Null 1	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + \varepsilon_{tij},$ $j = 1,...,n, \quad i = 1,...,n_j, \quad t = 1,...,n_{ij}$ $\alpha_j \sim N(0,\sigma_1^2), \quad \alpha_{ij} \sim N(0,\sigma_2^2), \quad \varepsilon_{tj} \sim N(0,\sigma^2).$	Increment width (G_{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	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + \alpha_{tj} + f(A_{tij}) + \varepsilon_{tij}$, $j = 1,...,n, \quad i = 1,...,n_j, \quad t = 1,...,n_{ij}$ $\alpha_j \sim N(0,\sigma_1^2), \ \alpha_{ij} \sim N(0,\sigma_2^2), \ \alpha_{tj} \sim N(0,\sigma_3^2), \quad \varepsilon_{tij} \sim N(0,\sigma^2).$	As above, but now containing crossed random factors; the random effect of growth year t is nested within river system j.
Spatial, intrinsic and extrinsic effects		
E1	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + f(F_{tij},A_{tij}) + \varepsilon_{tij}$, $j = 1,...,n, \quad i = 1,...,n_j, \quad t = 1,...,n_{ij}$ $\alpha_j \sim N(0,\sigma_1^2), \ \alpha_{ij} \sim N(0,\sigma_2^2), \ \varepsilon_{tij} \sim N(0,\sigma^2).$	Null 1 + curvilinear effects induced by the interaction between standardised discharge and age.
E2	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + f(T_{tij},A_{tij}) + \varepsilon_{tij}$, $j = 1,...,n, \quad i = 1,...,n_j, \quad t = 1,...,n_{ij}$ $\alpha_j \sim N(0,\sigma_1^2), \ \alpha_{ij} \sim N(0,\sigma_2^2), \ \varepsilon_{tij} \sim N(0,\sigma^2).$	Null 1 + curvilinear effects induced by the interaction between mean maximum daily temperature and age.
E3	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + f(F_{tij},A_{tij}) + f(T_{tij},A_{tij}) + \varepsilon_{tij}$, $j = 1,...,n, \quad i = 1,...,n_j, \quad t = 1,...,n_{ij}$ $\alpha_j \sim N(0,\sigma_1^2), \ \alpha_{ij} \sim N(0,\sigma_2^2), \ \varepsilon_{tij} \sim N(0,\sigma^2).$	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	$G_{tij} = \alpha + \alpha_j + \alpha_{ij} + f(A_{tij}) + f(F_{tij},A_{tij}) + f(T_{tij},A_{tij}) + f(F_{tij},T_{tij},A_{tij}) + \varepsilon_{tij}$, $j = 1,...,n, \quad i = 1,...,n_j, \quad t = 1,...,n_{ij}$ $\alpha_j \sim N(0,\sigma_1^2), \ \alpha_{ij} \sim N(0,\sigma_2^2), \ \varepsilon_{tij} \sim N(0,\sigma^2).$	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.
Spatial, intrinsic and extrinsic effects, including temporal autocorrelation		
E5-E8	Formulae E5-E8 follow E1-E4, respectively, but with a first-order correlation structure of residuals across growth years, such that: $$\text{cor}(\varepsilon_s,\varepsilon_t) = \begin{cases} 1 & \text{if } s = t \\ \rho^{|t-s|} & \text{else} \end{cases}$$	Descriptions as for E1-E4, 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 their

1061 Akaike Information Criteria (AIC; decreasing log-likelihood (Log(L)). Δ_i = AIC_i – min(AIC) is the

1062 AIC model rank; and w_i is the Akaike weight of model i, interpreted as the approximate probability

1063 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 temporal

1068 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).

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

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

$$\alpha_j \sim N(0,\sigma_1^2), \quad \alpha_{ij} \sim N(0,\sigma_2^2), \quad \varepsilon_{tj} \sim N(0,\sigma^2) \qquad \text{cor}(\varepsilon_s,\varepsilon_t) = \begin{cases} 1 & \text{if } s = t \\ \rho^{|t-s|} & \text{else} \end{cases}$$

$R^2 = 0.82$	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	

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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

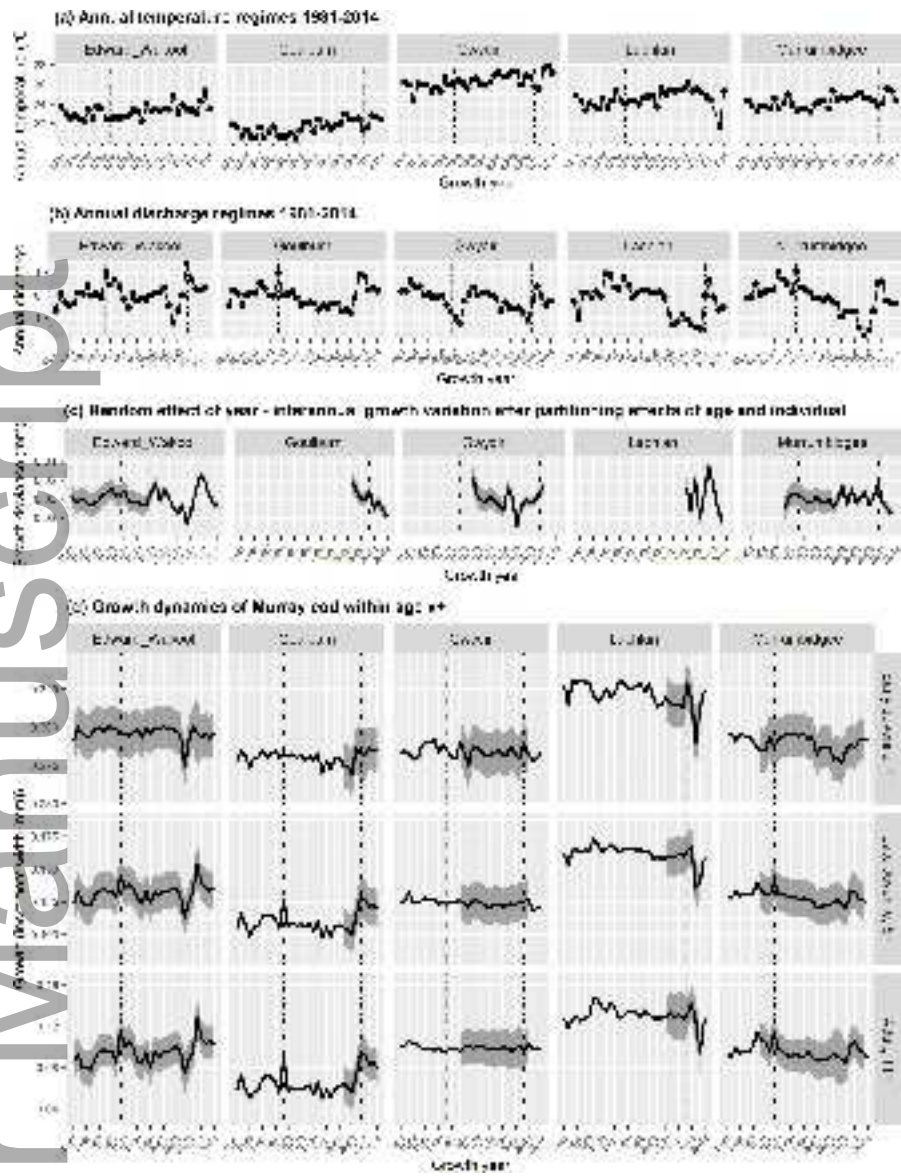1097   statistical uncertainty ('Discharge + Statistical'). Annual temperatures are in degrees Celsius.
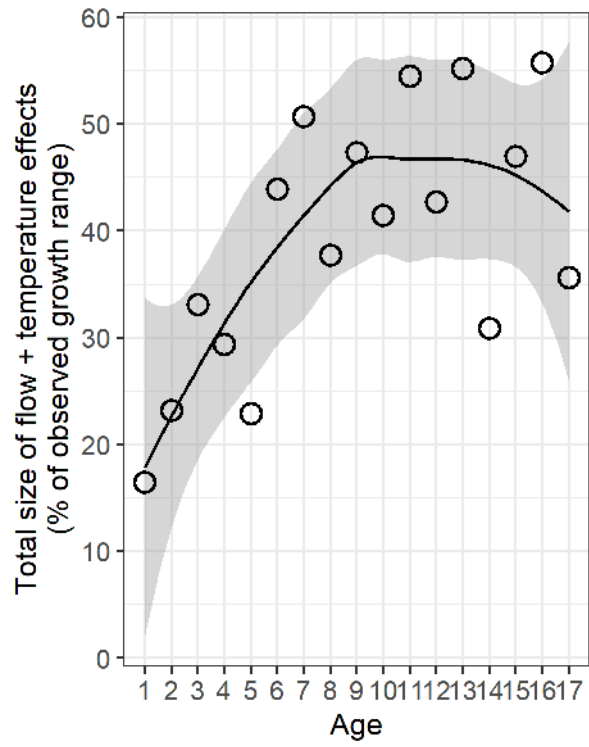
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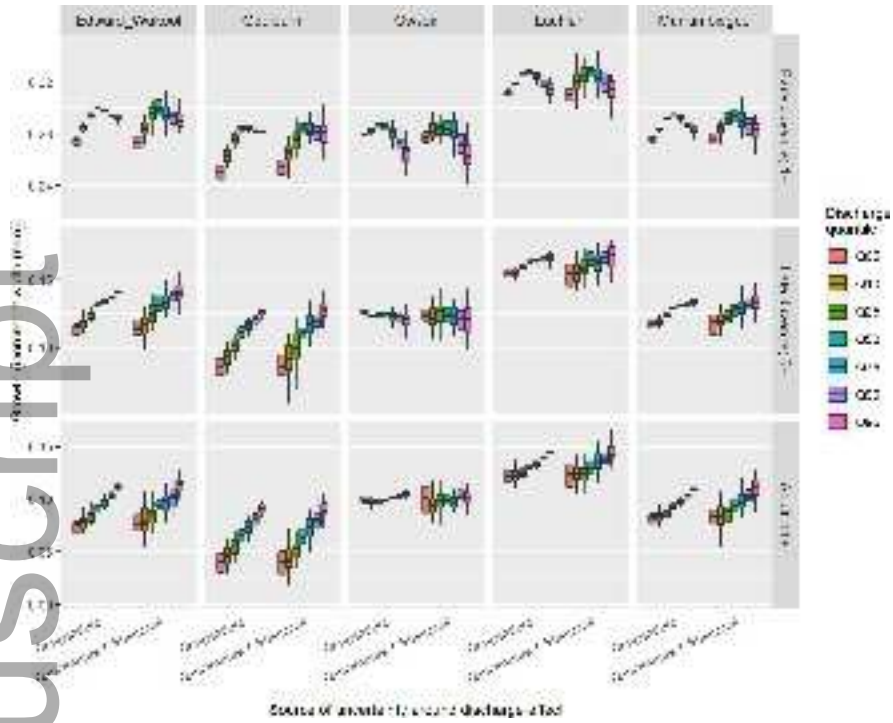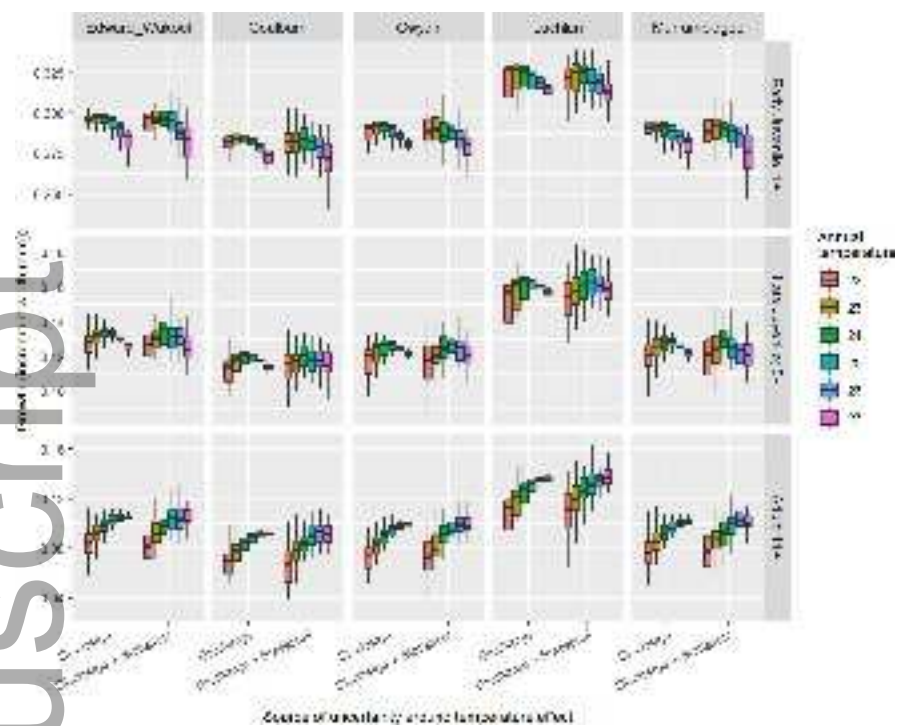
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