Changing patterns of growth in a changing planet: how a shift in phenology affects critical life-history traits in annual fishes

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Summary

23

24 1. Under current climate change trends, freshwater wetlands in the temperate

25 Neotropics are predicted to undergo major alternations in precipitation regime.

26 2. We investigated consequences of altered seasonal patterns in precipitation on

27 replicated populations of annual killifish, using a field survey. Annual killifish are

28 endemic to ephemeral pools and highly endangered through disruptions to wetlands.

29 3. In 2015, the Pampa region of western Uruguay experienced an unprecedented mid-

30 winter desiccation of temporary pools that naturally contain water from autumn to late

31 spring and typically only desiccate in summer. In our study area, 72% of desiccated

32 pools were re-inundated from later rains and annual killifish hatched a second cohort in

33 some of them (53%).

34 4. Compared to the first cohort, the second cohort experienced lower water

35 temperatures during hatching and juvenile development, but higher temperatures during

36 the adult growth phase. The second cohort of fish developed more rapidly, with 40%

37 earlier attainment of asymptotic body size (14 vs. 23 weeks) that was significantly

38 smaller in one species (*Austrolebias bellottii*) but not in the other (*Austrolebias*

39 *nigripinnis*).

40 5. Rapid juvenile development of second-cohort fish was associated with earlier

41 maturation and greater investment in reproductive tissue. The abbreviated life history

42 was adaptive because second-cohort fish lived shorter lives due to high summer

43 temperatures desiccating pools and extirpating the annual populations.

44 6. Annual fish demonstrated high developmental plasticity that buffered the negative

45 consequences of a severely altered seasonal climatic cycle. The capacity of these annual

46   fishes to cope with alternations to their life cycle will depend on the ability of egg banks

47   in the sediment to tolerate an increased unpredictability of precipitation.

1. INTRODUCTION

Current climate change trends are rapidly driving modifications to the temporal and spatial distribution of temperature and precipitation across the planet (Trenberth, 2011; Walther *et al.*, 2002). These changes can affect biodiversity at all levels, from individual populations to biomes (Parmesan, 2006). Some of the most striking effects of climate change are alterations in species phenologies; changes in timing of crucial life cycle events. This effect may lead to cascading effects at the community level (Edwards & Richardson, 2004; Gilman *et al.*, 2010), through the responses of interacting species (Bellard *et al.*, 2012). Changes in plant phenology, for example, can affect pollinator populations. Given their mutual dependency, altered plant phenology may ultimately lead to the extinction of both pollinators and plants (Rafferty & Ives, 2010). However, a range of other effects on the relationships between affiliate species can emerge (Rafferty *et al.*, 2014; Hassall *et al.*, 2019), with largely unknown capacity for resilience in some taxa (Hegg *et al.*, 2013).

Changes in species phenology may also lead to changes in life history traits, which determine the way an individual spreads its reproduction over its lifetime (Forrest & Miller-Rushing, 2010). For example, delayed hatching time can lead to post-hatching development under altered environmental conditions, shifting growth and maturation patterns, with potential consequences for the viability of subsequent generations (Varpe, 2017). In Atlantic salmon (*Salmo salar*), date of emergence of offspring has consequences for juvenile body size, with a significant decrease in juvenile body size at the end of the growing season in individuals that emerged one week later than the first cohort. This outcome may affect size-selective events, such as winter mortality, predation risk and reproduction (Einum & Fleming, 2000). Other ecological challenges can alter key life-history events. Interspecific resource

73 competition can ultimately affect growth patterns and timing of sexual maturation

74 (Ferreira-Rodríguez *et al*., 2018) to a degree that surpasses the effects of climate

75 (Rolinson *et al*., 2016). Therefore, it is important to compare the relative importance of

76 one ecological challenge (climate change) with other potential modulators of life-

77 history events.

78   The effects of altered phenology are likely to be especially pronounced in

79 ephemeral environments. Temporary habitats are subject to shifts between alternative

80 habitat states, often predictably following annual cycles of precipitation and

81 temperature (Varpe, 2017). Temporary pools are extreme environments that depend on

82 natural seasonal cycles between aquatic and desiccated phases (Polačik & Podrabsky,

83 2015). Among the organisms exploiting these environments, many are exclusively

84 adapted to the periodic phases of the habitat. In some cases, selection favours adaptation

85 to the regular pattern of aquatic phases, such as annual spring flooding (Lytle & Poff,

86 2004), though other species appear adapted to the unpredictability of erratic events,

87 such as desert flooding (Polačik & Podrabsky, 2015). As climate change modifies

88 precipitation regimes and increases the incidence of temporarily abbreviated rainfall

89 and concomitant extended periods of drought and heavy rainfall (Witze, 2018),

90 temporary pools experience dramatic change in their seasonal patterns of aquatic and

91 desiccated phases (Brooks, 2009). How these changes might alter the viability of

92 populations occupying these environments has yet to be explored.

93   Annual killifishes are a unique group of vertebrates that is exclusively adapted

94 to live in temporary pools. In the Neotropics and Africa, killifishes

95 (Cyprinodontiformes) have repeatedly adapted to life in ephemeral freshwater habitats

96 (Furness, 2016), with three independent evolutionary transitions to adopt this life

97 history in the family Rivulidae (Furness *et al.*, 2015a), a Neotropical clade of

98   Cyprinodontiformes fishes (Loureiro *et al.*, 2018). Populations of annual fishes persist

99   in desiccated sediment in the form of embryos encased in eggs with a thickened chorion.

100   Development is halted in three diapause stages (Wourms, 1972) when the embryo is

101   particularly resilient to environmental stress (Podrabsky *et al.*, 2001). Fish hatch when

102   their natal pool is filled with water. After hatching they grow rapidly and reach sexual

103   maturity within a few weeks (Vrtílek *et al.*, 2018). Adults reproduce daily and the eggs

104   are deposited into the substrate where they survive until a subsequent aquatic phase.

105   The timing of embryo development is variable, with a marked differential propensity

106   of embryos to enter and leave diapause (Wourms, 1972; Podrabsky & Hand, 1999;

107   Furness *et al.*, 2015b; Polačik *et al.*, 2018), though it is broadly synchronised by

108   environmental cues (Domínguez-Castanedo *et al.*, 2017), including temperature

109   (Podrabsky *et al.*, 2010a), photoperiod (Levels & Denucé 1988) and relative humidity

110   (Podrabsky *et al.*, 2010b).

111   Neotropical annual killifish are highly endangered. The major recognized threat

112   to their populations in southern South America (the Pampas biome) is habitat loss

113   associated with extensive agriculture and floodplain regulation (Volcan & Lanés, 2018).

114   In addition, annual fish depend on specific precipitation patterns and may be strictly

115   adapted to local natural cycles of pool inundation and desiccation. In southern South

116   America, the natural aquatic phase begins in the austral autumn (April), when

117   evaporation decreases and pools retain water from precipitation. The dry phase begins

118   in late spring (November), when evaporation increases and exceeds precipitation, and

119   habitats desiccate. Hence, unlike in the tropical range of annual fishes in Africa

120   (Reichard, 2016) and the Neotropics (Domínguez-Castanedo *et al.*, 2013; Podrabsky *et*

121   *al.*, 1997), there are no distinct rainy and dry seasons, and precipitation (with substrate

122 wetting and short-term accumulation of water) is relevant throughout the dry season,

123 though precipitation does not lead to an aquatic phase during the summer months.

124   With recent changes in climatic conditions, we have earlier reported (García *et*

125 *al.*, 2018) that the lower Río Negro floodplain (Villa Soriano district in western

126 Uruguay, Pampa vegetation region) experienced an unusual desiccation of temporary

127 pools in the middle of the aquatic phase (austral winter) in 2015, followed by an

128 unusually heavy precipitation that re-filled most of the desiccated pools. This event

129 triggered the hatching of a new cohort of annual fish in some pools (García *et al.*, 2018).

130 Here, we tested how the alteration of seasonal patterns affected the growth, maturation

131 and fecundity of these anomalous annual fish populations. The region of South

132 American pampas, to which more than 40 species of annual killifish are endemic

133 (Froese & Pauly, 2018), experienced a moderate increase in temperature and more than

134 30% decrease in precipitation between 1976 and 1990 (Walther *et al.*, 2002). This area

135 belongs to a region with the fastest estimated temperature increase (Loarie *et al.*, 2009).

136 Periods of heavy rains are predicted to increase in the region of between 20 - 50% in

137 the next 90 years with a 3 °C increase in global temperature (Fisher & Knuti, 2015;

138 Witze, 2018).

139   We investigated how the growth rate and sexual maturation of two annual

140 killifish species, *Austrolebias bellottii* and *A. nigripinnis*, were affected by non-

141 seasonal conditions (a second cohort that hatched in mid-winter rather than in autumn)

142 and compared it with the effects of another ecological challenge, interspecific

143 competition. Growth and maturation are crucial life history traits for individual fitness

144 (Stearns, 1992) and population dynamics (Sæther & Bakke, 2000) and this is especially

145 pronounced in short-lived annual fishes (Wootton & Smith, 2015; Vrtílek *et al.*, 2018).

146 We compared the growth and maturation of replicated *A. bellottii* populations

147   coexisting with *A. nigripinnis* and replicated *A. bellottii* populations without intra-guild

148   interspecific competition. Then, as the main goal of the study, we compared the growth

149   and development between the two cohorts of *A. bellottii* and the timing and size at

150   maturation of both cohorts and for each species. We predicted slower growth and later

151   sexual maturation in populations of *A. bellottii* coexisting with *A. nigripinnis* as a result

152   of interspecific competition between species occupying a similar ecological niche

153   (Arim *et al.*, 2010). Based on life history theory, we further predicted that the second

154   cohort (with a shorter expected lifespan) would trade somatic growth for a greater

155   reproductive effort (Figueredo *et al.*, 2006). Thus, individuals of the second cohort were

156   predicted to reach a smaller final size but mature earlier than the first cohort and make

157   a greater investment into reproduction than the first cohort, which was predicted to

158   divert more resources to a longer growth phase resulting in higher lifetime fecundity.

159

160   **2. Methods**

161   **2.1. Study area**

162   The study was conducted in the surroundings of Villa Soriano in Uruguay (33°23'56"S,

163   58°19'13"W) in 2015. This is a wetland area of a typical Pampa biome. It is

164   characterized by low altitude (1-7 m above sea level) and an abundance of shallow

165   temporary freshwater pools. The pools are from 100 to over 2,000 m^2 in area, with a

166   maximum depth of 0.4 m. Annual killifish (three species) are regularly encountered in

167   the pools. Other fish species invade the pools sporadically, following flooding from the

168   adjacent Rio Negro. The study area encompassed approximately 53 km^2. For a detailed

169   description of the study area see García *et al.* (2018).

170   The study is based on sampling in 18 pools (Fig. 1). The annual fish that inhabit

171   the area are *Austrolebias bellottii*, *A. nigripinnis* and *A. elongatus*. Thirteen pools (72%)

172 were re-inundated but the second cohort of *A. bellotti* hatched only in 6 of 18 (33%)

173 and *A. nigripinnis* in 7 pools (39%). No second cohort hatched after re-inundation in

174 the 6 pools. The first cohort persisted throughout winter in XXX pools (*A. bellottii*) and

175 YYY pools (*A. nigripinnis*). Given the rare occurrence of *A. elongatus* (0.23% of

176 sampled fish in a total of 17% of the pools), this study focused on the other two species.

177

178 **2.2. Sampling and data collection**

179 Sampling started on 18 May 2015 and lasted until no further fish could be collected or

180 pools were dry (1 January 2016). Sampling was conducted every two weeks, except for

181 a 20-day interval between trip 7 (9–10 Aug) and trip 8 (29 Aug–1 Sep). For all pools,

182 fish hatching dates were estimated from otolith increments and the age of the fish was

183 calculated by adding the number of days between sampling trips. The first cohort

184 hatched in late April and the second cohort hatched in early August in some pools that

185 experienced mid-season desiccation (García *et al.*, 2018). The pools were at least 0.3

186 km apart, except for pools 11D and 12D that were only 0.1 km apart but clearly separate.

187 Detailed descriptions of seasonal dynamics in population density and abundance are

188 described in García *et al.* (2019). In short, for the period of juvenile growth the pool

189 area was larger in the second cohort, but fish density was comparable between the

190 cohorts. Water temperature data were collected by data loggers (Hobo UA-002-08)

191 deployed in 12 pools on the first day of sampling. The loggers also provided the timing

192 of pool desiccation (Lanés *et al.*, 2016; García *et al.*, 2018).

193 Sampling was accomplished with a dip-net (200 x 150 mm, 2 mm mesh size)

194 that was swept parallel to the bottom. All available habitats in the pool were explored.

195 Sampling effort varied across sites due to wide variation in fish density and pool area.

196 Sampling effort was recorded as time spent collecting fish (median = 26 min, mean =

197   32, standard deviation = 23.8) and pool surface area. Pool area was measured *in situ*

198   during each sampling event by walking around the pool boundaries using a portable

199   GPS unit to map the outline of the pool surface (Garmin Etrex10). After sampling, all

200   annual fish collected were photographed on a tray (80 x 80 mm) with a wetted surface

201   and a reference scale. A total of 4,804 *A. bellottii* and 2,592 *A. nigripinnis* were

202   measured. Sample size for each pool, species, sex, and sampling event is given in

203   Supporting Information (Table S1). A random sample of 5 females was taken at each

204   sampling to estimate sexual maturation. Fish were euthanized with an overdose of clove

205   oil and stored in 4% formaldehyde for later dissection in the laboratory. All other fish

206   were then returned to the pool. Species and sex were determined from photographs on

207   the basis of external characters (fin size, shape and colouration). Size of fish was

208   measured from photographs using *tpsDig2* software (v 2.1) (Rohlf, 2009) from the tip

209   of the snout to the end of the caudal fin (Total Length, TL). In the laboratory, a sample

210   of 5 females was measured for TL, weighed (W, to the nearest of 0.001g), dissected

211   and gonad mass (Wg) measured.

212   **2.3. Data analysis**

213   All analyses were completed in the R statistical environment (R Core Team, 2018).

214   First, we tested the effects of the presence of *A. nigripinnis* on the growth patterns of *A.*

215   *bellottii*. *Austrolebias bellottii* was present in all pools but *A. nigripinnis* occurred only

216   in 55% of pools (10 of 18). We used sex-specific Generalised Additive Mixed Models

217   (GAMM) with a Gaussian error distribution, with Coexistence (factor with two levels)

218   included as a fixed effect. The effect of age was modelled with a smoother term with 5

219   knots (k = 5), defined *a priori* based on the growth trajectory of *Austrolebias* (Volcan

220   *et al.*, 2012) and allowing for potential selective disappearance of larger fish at the end

221   of the season (Reichard *et al.*, 2018). The response variable was body size, measured

222 as TL. To account for dependency in the data from variation among pools, pool identity

223 was included as random effect. Two models were constructed that differed in how the

224 smoother term was modelled. First, a separate smoother was assigned for each

225 treatment level (coexistence with *A. nigripinnis* or not). Second, the same smoother was

226 used for both treatments. The fit of the models was compared using Akaike Information

227 Criterion (AIC). An AIC difference of   >10 is considered a substantial improvement

228 in model fit. GAMM analysis was completed in the *gamm4* package (Wood & Scheipl,

229 2017).

230 Similarly, we compared whether coexistence with *A. nigripinnis* affected time

231 to sexual maturity in *A. bellottii* females. Because a high proportion of fish were

232 immature, data were modelled using a zero-altered (hurdle) model, using   R-INLA

233 (Rue *et al*., 2017). Zero-altered models are partitioned into two parts, with a binary

234 process modelling zeros and positive counts, and a second process modelling only

235 positive counts using a zero-truncated model (Hilbe, 2014). We modelled zero-

236 truncated data using a Gaussian distribution (Zuur *et al*., 2014). This approach enabled

237 us to separately identify the environmental variables that predicted maturity (binary

238 part) and investment in gonad mass when gonads were present (zero-truncated part).

239 Fixed factors were Coexistence (two levels), body size (TL, log-transformed,

240 continuous predictor) and their interaction. In the model, the interaction between

241 Coexistence and TL measured the contribution of species coexistence to the timing of

242 sexual maturation relative to body size. This analysis was based on a contrast between

243 6 populations of *A. bellottii* without *A. nigripinnis* and 5 populations of *A. bellottii*

244 competing with *A. nigripinnis*, with four populations dropped during data exploration

245 due to the small number of females analysed (≤ 5).

246   The main analysis compared growth trajectories and sexual maturation of fish

247   from the first and second cohort, using the same approach as for testing the effect of

248   coexistence. We predicted, *a priori*, that the two species and sexes within species,

249   would differ in body size (Costa, 2006) and, consequently, we separated them before

250   analysis. We fitted sex-specific GAMMs with a Gaussian error distribution that

251   included the factor Cohort (two levels). Given that the coexistence of *A. bellottii* with

252   *A. nigripinnis* had no effect on growth and sexual maturation, this factor was not

253   included in the analysis. We modelled age either with separate smoothers for each

254   cohort (model 1) or a common smoother for both cohorts (model 2), with k = 5 in both

255   models. The fit of the two models was compared using AIC. The same analysis was

256   performed for both fish species.

257   To formally test the differences in the growth rates (rather than size at age)

258   among cohorts, we calculated Specific Growth Rates (SGR) using the function:

259
$$SGR = (\ln(TL_x) - \ln(TL_{x-1}) \times \frac{100}{N_{days}})$$

260   Where TL_x is the Total Length for the date *x*, TL_{x-1} is the Total Length for the previous

261   date and N_{days} is the number of days between each date. SGR was estimated for each

262   species and each pool separately. We tested whether SGR differed between cohorts by

263   fitting a Gaussian Linear Model (LM) with age interval, cohort and their interaction as

264   factors. The response variable was population-specific SGR. Given the shorter lifespan

265   of the second cohort, we truncated age intervals for the first cohort to permit a full

266   interaction between the two factors. This analysis was completed for *A. bellottii* only

267   because we had insufficient estimates of population-specific SGR for the first cohort of

268   *A. nigripinnis*. For visualization, we extended estimated SGR for the first cohort over

269   their entire lifespan.

270   While growth curves are commonly used in analysing growth data, they suffer

271   from temporal dependency. To formally accommodate temporal dependency in the data,

272   we further modelled fish size using a random walk (RW2) trend model in a Bayesian

273   framework using Integrated Nested Laplace Approximation (R-INLA; Rue *et al.*, 2017).

274   Fish size was fitted for fish age following a gamma distribution with a log link function.

275   The model was fitted as:

276
$$TL_{ijk} \sim N(\mu_{ijk}, \tau)$$

277
$$E(TL_{ijk}) = \mu_{ijk} \text{ and } var(TL_{ijk}) = \frac{\mu_{ijk}^2}{\tau}$$

278
$$\log(\mu_{ijk}) = \eta_{ijk}$$

279
$$\eta_{ijk} = \beta_1 + \beta_2 \times Sex_{ijk} \times \beta_3 \times Coh_{ijk} + \beta_4 \times Area_{ijk} + Age_j + Pool_k$$

280
$$Age_j \sim N(0, \sigma_{Age}^2)$$

281
$$Pool_k \sim N(0, \sigma_{Pool}^2)$$

282   Where TL_{ijk} is the size of fish i of age (*Age*) j. The variable Sex_{ijk} is a categorical

283   covariate with two levels (males, females) and Coh_{ijk} is a categorical covariate with two

284   levels (first or second cohort). The model also contained a linear effect for pool size

285   ($Area_{ijk}$) as its extent varied over the season. The random intercept *Pool* was included

286   in the model to introduce a correlation structure between observations for fish collected

287   from the same pool with variance σ^2, distributed normally and equal to 0. Uniform

288   default priors were put on model parameters and fitted estimates of fish size matched

289   observed data.

290   Time to sexual maturation and investment in reproduction were compared

291   between cohorts using data on gonad mass (Wg) fitted with a zero-adjusted model with

292   a gamma distribution (ZAG), like that used for interspecific competition contrasts. All

293 final models were checked for overdispersion and model mis-specification following

294 the guidelines of Zuur & Ieno (2016).

295

296 **3. RESULTS**

297 **3.1. Effect of interspecific competition**

298 There was no major effect of inter-specific competition on the growth of *A. bellottii*

299 (GAMM, males: $F = 0.12$, $P = 0.77$; females: $F = 1.27$, $P = 0.260$), with a clearly inferior

300 fit of the separate-smoothers model for females ($\Delta AIC = +256$). In males, the model

301 with separate smoothers for males provided a better fit ($\Delta AIC = -10.3$), though the

302 principal difference was that the separate-smoothers model captured differences in size-

303 selective mortality at the terminal phase of life rather than different growth rates among

304 *A. bellottii* populations coexisting with *A. nigripinnis* (Fig. 2). There was no effect of

305 coexistence with *A. nigripinnis* on the timing of sexual maturity of *A. bellottii* females

306 (binary part of the model) or their allocation to gonads (zero-truncated part). Female *A.*

307 *bellottii* maturation and allocation to reproduction depended on body size but the

308 scaling of the relationship did not differ between coexistence treatment levels (Table

309 1).

310 **3.2. Differences between the two cohorts**

311 **3.2.1. Water temperature**

312 The first cohort experienced a temperature regime typical of temporary pools in the

313 region. Water temperature decreased from warm (>20°C) to cold (<10°C) over the early

314 life phase, remained relatively cold until the age of approximately 100 days and slowly

315 climbed to 20°C again over the subsequent 100 days (Fig. 3). The second cohort

316 hatched in relatively colder water that steadily increased in temperature and never fell

317 below 10°C (Fig. 3).

3.2.2. Growth trajectories

319 There were clear differences in growth trajectories of the first and second cohorts of

320 both species, except for *A. nigripinnis* females. The models with separate smoothers for

321 each cohort were clearly superior in *A. bellottii* males (ΔAIC = -118), *A. bellottii*

322 females (ΔAIC = -246) and *A. nigripinnis* males (ΔAIC = -39), but only marginally in

323 *A. nigripinnis* females (ΔAIC = -2.52). The growth curves were characterised by earlier

324 attainment of the growth asymptote in the second cohort (approximately 100 days) than

325 in the first cohort (approximately 150-170 days) (Fig. 4), resulting in a larger mean

326 asymptotic size in *A. bellottii* (males: F = 19.79, P < 0.001, Fig. 4a; females: F = 16.16,

327 P < 0.001; Fig. 4b) but not *A. nigripinnis* (Fig. 4c, 4d).

328 Comparing specific growth rates (SGR) confirmed a steeper growth trajectory

329 of second cohort fish over age-matched categories (LM: $F_{1,71}$ = 4.67, P = 0.024) and

330 much stronger decline in the SGR with age in the second cohort fish (age by cohort

331 interaction: $F_{1,71}$ = 12.42, P = 0.001; age: $F_{1,71}$ = 3.28, P = 0.074) (Fig. 5). Overall, SGRs

332 were initially higher in the second cohort but declined sharply with age. In contrast, the

333 growth rates of the first cohort were relatively stable, though they varied among

334 populations (Fig. 5).

3.2.3. Body size

336 Fitting a common smoother to growth data for *A. bellottii* using a gamma random walk

337 trend model fitted using INLA demonstrated that sex differences in body size were

338 higher in the second cohort (sex by cohort interaction in Table 2) and quantitatively

339 confirmed that the second cohort grew more quickly (Cohort effect in Table 2).

340 **3.2.4. Sexual maturation**

341 Female maturation was strongly positively related to age (binomial occurrence model)

342 with a steeper increase in the second-cohort females (Table 3a), implying that second-

343 cohort fish reached sexual maturation at a younger age. In addition, the frequency

344 model (magnitude of gonadal investment) demonstrated that the second-cohort females

345 invested more heavily in gonad mass. Greater gonad mass was also recorded from pools

346 with a larger area. As expected, gonad mass was positively associated with female age

347 (Table 3b).

348

349 **4. Discussion**

350 The primary effects of climate change are alterations in precipitation and temperature

351 dynamics which have profound implications for species phenologies (Parmesan, 2006;

352 Ficetola & Maiorano, 2016). However, responses to climate change and its

353 consequences potentially vary greatly among species (Both *et al.*, 2009; Colchero *et al.*,

354 2019) and among particular interspecific interactions (Gilman *et al.*, 2010; Kordas *et*

355 *al.*, 2011; Hassall *et al.*, 2019). We demonstrated previously that *Austrolebias* annual

356 fishes are able to hatch a new cohort in response to a secondary inundation following

357 an unexpected mid-winter (July) pool desiccation, though a second cohort hatched only

358 in a subset of pools (García *et al.*, 2018). In the present study, we tested the

359 developmental consequences of late season hatching in an environment with a non-

360 optimal temperature regime in *A. bellottii*. Overall, the changes associated with late

361 hatching demonstrated the capacity of *A. bellottii* to cope with shifted seasonality and

362 to adjust their life history to maximize reproductive success. Following non-seasonal

363 desiccation and subsequent re-filling of pools, 46% (6 of 13) *A. bellottii* populations

hatched a second cohort. The second-cohort juveniles developed in colder water (until the age of approximately 50 days) but sustained accelerated growth and more rapid sexual maturation, along with a greater investment in fecundity. While this came at the cost of smaller final size, the response was adaptive since life expectancy (and actual lifespan) in the second cohort was shorter. The magnitude of response was substantial, with no effects on growth and sexual maturation in populations subjected to another ecological challenge, interspecific competition with *A. nigripinnis*, a related annual killifish species that coexisted in several pools with *A. bellottii*. *Austrolebias nigripinnis* also experienced accelerated growth in the second cohort, though the effect was marginal in *A. nigripinnis* females and their asymptotic size was not smaller.

Differences in growth rate, final size and sexual maturation were most likely shaped by the different temperature dynamics experienced by juvenile and adult *A. bellottii*. The first cohort experienced typical seasonal dynamics in water temperature, with hatching and the juvenile period during warm-water conditions in the austral autumn (April), followed by a gradual decrease in temperature with adults living in a low temperature environment during winter and experiencing increased mortality in late spring (November) as the temperature again increased (García *et al.*, 2019). Those conditions are typical for most *Austrolebias* populations (Lanés *et al.*, 2016). The second cohort hatched in cold water with the temperature steadily increasing over the season and exposing young adults (5 months old) to ambient temperatures exceeding 25°C (Fig. 3), which is considered the upper limit for the long-term survival of *Austrolebias* (Lanés *et al.*, 2016). In addition, the cohorts experienced different photoperiods. While both cohorts hatched in a photoperiod of 10.5-11 hours of daylight, this period decreased by 1 hour over two months of juvenile growth for the first cohort, but increased by 2 hours for the second cohort, respectively (www.sunrise-sunset.org).

389   Increasing water temperature and photoperiod might have also increased productivity

390   of the pools, further stimulating more rapid growth of the second cohort. Pools were

391   generally larger after the second inundation, but killifish population densities were

392   comparable (García *et al.*, 2019).

393   Laboratory studies have demonstrated that annual fishes are sensitive to

394   temperature regimes (Hsu & Chiu, 2009; Volcan *et al.*, 2012; da Fonseca *et al.*, 2013).

395   *Austrolebias adloffii*, a related species from the same region, exhibited a decreased

396   growth rate and shorter lifespan when a natural decrease in water temperature

397   fluctuation was interrupted. After rearing juveniles at 22°C, a decrease in temperature

398   (to 16°C) was associated with longer lifespan and sustained growth while control fish

399   that remained at 22°C ceased growing (Liu & Walford, 1966). Our field data are

400   consistent with laboratory studies of *Austrolebias* that reported earlier sexual maturity

401   and more rapid growth at higher temperature (25°C compared to 15°C in *Austrolebias*

402   *viarius*, and 22°C compared to 16°C in *Austrolebias nigrofasciatus*) (Errea & Danulat,

403   2001; Volcan *et al.*, 2012). However, the positive correlation between water

404   temperature and juvenile development is reversed when temperature exceeds an

405   optimum of 21-24°C in *Austrolebias wolterstorffi* (Fonseca *et al.*, 2013). High ambient

406   temperature during the juvenile growth phase comes at the cost of shorter lifespan

407   (Errea & Danulat, 2001). Thermal optima of *Austrolebias* are age-specific and

408   persistent high ambient temperature is costly to adult fish (Walford & Liu, 1965; Liu &

409   Walford, 1966).

410   We observed selective disappearance of larger individuals from populations

411   during the terminal phases of growth (Fig. 4), though this may partly indicate selective

412   predation (Reichard *et al.*, 2018) or limited endurance of large males contingent upon

413   their investment in courtship and reproductive activity (Passos *et al.*, 2014) rather than

414   from a direct trade-off between rapid growth and longevity. Hence, while longevity of

415   annual fishes is associated with lower ambient temperature (Walford & Liu, 1965;

416   Valenzano *et al.*, 2006; Hsu & Chiu, 2009), *A. bellottii* can cope with an altered

417   seasonal trend in water temperature and appears able to respond with an adaptive

418   increase in developmental rate and higher reproductive allocation. Second-cohort

419   females invested in early reproduction with earlier sexual maturation and greater

420   allocation to gonad mass, at the expense of a longer growth phase and, hence, greater

421   investment in future reproduction. This outcome is concordant with predictions from

422   life-history theory (Stearns, 1992), with cues indicating shorter life expectancy

423   probably based on ambient temperature.

424   Populations of annual fishes survive drying of their environment in egg banks

425   deposited in desiccated pool substrate (Polačik & Podrabsky, 2015). Propagule banks

426   are essential for the long-term persistence of communities in temporary environments

427   (Brock *et al.*, 2003). In annual fishes, egg development is temporally staggered due to

428   facultative diapause stages. After fertilization, the embryos initially develop for a few

429   days and may be halted in Diapause I in the anoxic conditions of decaying pool

430   substrate. Upon resumption of development, embryos may respond to desiccation by

431   entering Diapause II and continue development if the substrate is moistened (Reichard

432   & Polačik, 2019). Importantly, different embryos respond to external cues to a different

433   degree (Furness, 2016; Polačik *et al.*, 2017), resulting in the egg bank consisting of

434   embryos at various stages of development. In the study pools, hatching of the second

435   cohort was possible because the egg banks contained embryos ready to hatch at the time

436   of secondary inundation. While we term that group a new cohort, we acknowledge that

437   the fish may have hatched from eggs that were laid during the first inundation and may

438   effectively represent a second "generation". Interestingly, the length of embryonic

439   development has important consequences for post-hatching life. In African annual

440   killifish, rapidly developing embryos hatched to individuals that grew more quickly

441   (and were larger than individuals from slowly developing embryos from the age of 6

442   days), but lived shorter lives, and attained a smaller final size (Polačik *et al.*, 2014).

443   While in that experiment, all fish experienced identical environmental conditions (i.e.,

444   temperature, food supply, density), the outcomes were consistent with our results from

445   the wild. This finding suggests that there is an interplay between environmental

446   conditions and intrinsic developmental (potentially epigenetic) processes that give rise

447   to the expressed phenotype.

448   An outstanding question is how frequent the mid-season desiccation of

449   temporary pools in the pampas region was in the past, and how reliably the alternation

450   of flooding regime matches changes in the pattern of precipitation. While we have

451   shown that annual fish populations can respond to these changes with a secondary

452   hatching, a high frequency of mid-season desiccation could rapidly exhaust egg bank

453   reserves. Our dataset for the study region only encompasses 10 years of precipitation

454   and temperature data (data provided by National Meteorology Institute, INUMET).

455   This time series demonstrates unusually dry conditions from February to July 2015

456   (which resulted in desiccation) (Supporting Information, Fig. S1) even in the context

457   of the already less predictable rainfall pattern in the last decade (Ding *et al.*, 2008). We

458   acknowledge that it is critical to understand whether the observed mid-season drought

459   was an exceptional and isolated event or represents a climatic trend and if so, how

460   repeated droughts will affect existing annual fish egg banks.

461   While climate change can alter the ecology of many species (Walther *et al.*,

462   2002; Evans & Wallenstein, 2014), potentially driving some towards extinction

463   (Thomas *et al.*, 2004), we show that *A. bellottii*, a representative species of a highly

464 endangered group of annual fishes, appears capable of coping with a sporadic seasonal

465 shift in rainfall patterns. This finding indicates that environmentally-triggered

466 phenotypic plasticity of life-history traits expressed by *A. bellottii* permits maintenance

467 of viable populations despite altered phenology (Nylin & Gottard, 1998, Colchero *et*

468 *al.*, 2019). In fact, *A. bellottii* has a relatively wide distribution and some populations

469 reach the Río Paraguay basin in northern Argentina (García *et al.*, 2012) where

470 precipitation seasonality is different to the study region and fish hatch when the water

471 temperature is warmer. Phenotypic plasticity is important for forecasting species

472 distributions in a climate change scenario (Valladares *et al.*, 2014; Duputié *et al.*, 2015)

473 and this is especially important for species with limited dispersal abilities such as annual

474 fishes (García *et al.*, 2012).

475   *Austrolebias* species are the top predators in their communities (Laufer *et al.*,

476 2009) and their potential disappearance from ephemeral pools may lead to a cascade of

477 effects (Paine, 1966; Baum & Worm, 2009) with unknown consequences for

478 community structure. While the primary effects of climate change (alternations in

479 precipitation and temperature dynamics) affect phenologies of certain species

480 (Parmesan, 2006; Ficetola & Maiorano, 2016), downstream consequences vary greatly

481 among communities (Both *et al.*, 2009; Gilman *et al.*, 2010; Kordas *et al.*, 2011; Hassell

482 *et al.*, 2019). For example, in the plankton communities of the North Sea, phenology of

483 primary producers (diatoms) is driven by photoperiod and hence unaffected by elevated

484 temperature while phenology of secondary (zooplankton) and tertiary (fish larvae)

485 consumers have moved forward by 10-45 days over a 45-year study period (Edwards

486 & Richardson, 2004). The resulting mismatch in trophic cascade has been implicated

487 in the decline of marine pelagic production, including commercially important fish

488 species (Edwards & Richardson, 2004). In contrast, a shift in the peak abundance of

489   caterpillars was successfully compensated by modulation of egg-laying date and other

490   life history characteristics in pied flycatchers (*Ficedula hypoleuca*) for which

491   caterpillars represent the main food source (Both & Visser, 2005).

492   Freshwater wetlands inhabited by *Austrolebias* populations are important for

493   ecosystem function, including water purification and carbon retention (Baron *et al.*,

494   2002). In our study region, freshwater wetlands inhabited by *Austrolebias* populations

495   are utilized for cattle ranching, often in proximity to agricultural plots. While cattle

496   ranching has no apparent negative effect on temporary pools, and *Austrolebias*

497   populations may even benefit from cattle ranching (Volcan *et al.*, 2016), the major

498   threat to *Austrolebias* fishes is an expansion of rice or soybean cultivation (Volcan *et*

499   *al.*, 2016; Volcan & Lanés, 2018). In Uruguay, agricultural development is primarily

500   associated with soybean, wheat and other crop, which have expanded as new

501   technologies have become available (Arbeletche & Gutiérrez, 2010; Dellazoppa, 2014).

502   The use of novel herbicides, for example, appears to alter the ability of *Austrolebias* to

503   cope with high water temperature, decreases their fecundity and affects diapausing

504   stages in the egg bank (Zebral *et al.*, 2018). In southern Brazil, rice cultivation alters

505   the natural flooding regime, with consequences reported for anuran and invertebrate

506   communities (Cuhna *et al.*, 2015; Ávila *et al.*, 2015) and with likely negative impacts

507   on annual fish populations. At present, changes to land use appear to overshadow any

508   negative consequences of climate change for *Austrolebias* fishes (Volcan & Lanés,

509   2018), though the interaction of these effects, which are difficult to predict, may

510   represent their greatest threat.

511

525

526   **Data Availability Statemen**t

527   Primary data are deposited at Figshare (doi: xxxx).

528 **References**

529 Arbeletche, P., & Gutiérrez, G. (2010). Crecimiento de la agricultura en Uruguay:

530   exclusión social o integración económica en redes. *Pampa* 6, 113-138.

531 Arim, M., Abades, S.R., Laufer, G., Loureiro, M., & Marquet, P. A. (2010). Food web

532   structure and body size: trophic position and resource acquisition. *Oikos*, 119(1),

533   147-153.

534 Ávila, A. C., Boelter, T., dos Santos, R. M., Stenert, C., Würdig, N. L., Rocha, O., &

535   Maltchik, L. (2015). The effects of different rice cultivation systems and ages on

536   resting stages of wetland invertebrates in southern Brazil. *Marine and Freshwater*

537   *Research*, 66(3), 276-285.

538 Baron, J. S., Poff, N. L., Angermeier, P. L., Dahm, C. N., Gleick, P. H., Hairston Jr.,

539   N. G., … Steinman, A. D. (2002). Meeting ecological and societal needs for

540   freshwater. *Ecological Applications*, 12(5), 1247-1260.

541 Baum, J. K., & Worm, B. (2009). Cascading top down effects of changing oceanic

542   predator abundances. *Journal of Animal Ecology*, 78(4), 699-714.

543 Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012).

544   Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15(4),

545   365-377. DOI: 10.1111/j.1461-0248.2011.01736.x

546 Blažek, R., Polačik, M., & Reichard, M. (2013). Rapid growth, early maturation and

547   short generation time in African annual fishes. *EvoDevo*, 4(1), 1–7. DOI:

548   10.1186/2041-9139-4-24

549 Both, C., Van Asch, M., Bijlsma, R. G., Van Den Burg, A. B., & Visser, M. E.

550   (2009). Climate change and unequal phenological changes across four trophic

551   levels: Constraints or adaptations? *Journal of Animal Ecology*, 78(1), 73–83. DOI:

552   10.1111/j.1365-2656.2008.01458.x

553   Both, C., & Visser, M. E. (2005). The effect of climate change on the correlation

554   between avian life history traits. *Global Change Biology*, 11(10), 1606-1613. DOI:

555   10.1111/j.1365-2486.2005.01038.x

556   Brock, M. A., Nielsen, D. L., Shiel, R. J., Green, J. D., & Langley, J. D. (2003).

557   Drought and aquatic community resilience: The role of eggs and seeds in

558   sediments of temporary wetlands. *Freshwater Biology*, 48(7), 1207–1218. DOI:

559   10.1046/j.1365-2427.2003.01083.x

560   Brooks, R. T. (2009). Potential impacts of global climate change on the hydrology

561   and ecology of ephemeral freshwater systems of the forests of the northeastern

562   United States. *Climatic Change*, 95(3-4), 469-483.

563   Cohen, J. M., Lajeunesse, M. J., & Rohr, J. R. (2018). A global synthesis of animal

564   phenological responses to climate change. *Nature Climate Change*, 8(3), 224–228

565   DOI: 10.1038/s41558-018-0067-3

566   Colchero, F., Jones, O., Conde, D. A., Hodgson, D., Zajitschek, F., Schmidt, B. R., ...

567   Gaillard, J. (2019). The diversity of population responses to environmental change.

568   *Ecology Letters*, 22, 342-353. DOI: 10.1111/ele.13195

569   Costa, W. J. E. M. (2006). The South American annual killifish genus *Austrolebias*

570   (Teleostei: Cyprinodontiformes: Rivulidae): phylogenetic relationships, descriptive

571   morphology and taxonomic revision. *Zootaxa*, (1213), 1-162.

572   Cunha, G. G., Stenert, C., Rolon, A., Mundstock, C. M., & Maltchik, L. (2015). Does

573   intensification of the rice cultivation cycle influence anuran diversity in rice fields?

574   *Wetlands ecology and management*, 23(4), 695-705.

575   Dellazoppa, R. (2014). *Agro La revolución sorprendente*. Montevideo, Editorial Fin

576   de Siglo.

577   Ding, R., Li, J., & Ha, K. J. (2008). Trends and interdecadal changes of weather

578   predictability during 1950s–1990s. *Journal of Geophysical Research:*

579   *Atmospheres*, 113(D24). DOI: 10.1029/2008JD010404

580   Domínguez-Castanedo, O., Mosqueda-Cabrera, M.Á., & Valdesalici, S. (2013). First

581   observations of annualism in *Millerichthys robustus* (Cyprinodontiformes:

582   Rivulidae). *Ichthyological Exploration of Freshwaters*, 24, 15-20.

583   Domínguez-Castanedo, O., Valdesalici, S., & Rosales-Torres, A. M. (2017).

584   Developmental ecology of annual killifish *Millerichthys robustus*

585   (Cyprinodontiformes: Cynolebiidae). *Developmental Dynamics*, 246(11), 802-806.

586   Duputié, A., Rutschmann, A., Ronce, O., & Chuine, I. (2015). Phenological plasticity

587   will not help all species adapt to climate change. *Global Change Biology*, 21(8),

588   3062-3073.

589   Edwards, M., & Richardson, A. J. (2004). The impact of climate change on the

590   phenology of the plankton community and trophic mismatch. *Nature*, 430(1977),

591   881–884.

592   Einum S., & Fleming, I. A. (2000). Selection against late emergence and small

593   offspring in Atlantic salmo (*Salmo salar*). *Evolution*, 54(2), 628–639.

594   Evans, S. E., & Wallenstein, M. D. (2014). Climate change alters ecological strategies

595   of soil bacteria. *Ecology Letters*, 17(2), 155-164.

596   Ferreira-Rodríguez, N., Sousa, R., & Pardo, I. (2018). Negative effects of *Corbicula*

597   *fluminea* over native freshwater mussels. *Hydrobiologia*, *810*(1), 85-95.

598   Ficetola, G. F., & Maiorano, L. (2016). Contrasting effects of temperature and

599   precipitation change on amphibian phenology, abundance and performance.

600   *Oecologia*, 181(3), 683-693.

601 Figueredo, A. J., Vásquez, G., Brumbach, B. H., Schneider, S. M. R., Sefcek, J. A.,

602   Tal, I. R., … Jacobs, W. J. (2006). Consilience and Life History Theory: From

603   genes to brain to reproductive strategy. *Developmental Review,* 26(2006), 243–

604   275. DOI: 10.1016/j.dr.2006.02.002

605 Fischer, E. M., & Knutti, R. (2015). Anthropogenic contribution to global occurrence

606   of heavy-precipitation and high-temperature extremes. *Nature Climate Change*,

607   5(6), 560-565.

608 Fonseca, A. P. D., Volcan, M. V., Sampaio, L. A., Romano, L. A., & Robaldo, R.B.

609   (2013). Growth of Critically Endangered annual fish *Austrolebias wolterstorffi*

610   (Cyprinodontiformes: Rivulidae) at different temperatures. *Neotropical*

611   *Ichthyology*, 11(4), 837-844.

612 Forrest, J., & Miller-Rushing, A. J. (2010). Toward a synthetic understanding of the

613   role of phenology in ecology and evolution. *Philosophical Transactions of the*

614   *Royal Society B: Biological Sciences*, 365(1555), 3101–3112. DOI:

615   10.1098/rstb.2010.0145

616 Froese, R., & Pauly, D. (2018). FishBase, version February 2018.

617 Furness, A. I. (2016). The evolution of an annual life cycle in killifish: adaptation to

618   ephemeral aquatic environments through embryonic diapause. *Biological Reviews*

619   *of the Cambridge Philosophical Society*, 91(3), 796–812. DOI: 10.1111/brv.12194

620 Furness, A. I., Reznick, D. N., Springer, M. S., & Meredith, R. W. (2015).

621   Convergent evolution of alternative developmental trajectories associated with

622   diapause in African and South American killifish. *Proceedings of the Royal Society*

623   *B: Biological Sciences*, 282(1802), 1–9. DOI: 10.1098/rspb.2014.2189

624 García, D., Loureiro, M., Machín, E., & Reichard, M. (2018). Phenology of three

625 coexisting annual fish species: seasonal patterns in hatching dates. *Hydrobiologia*,

626 809(1), 323-337.

627 García, D., Loureiro, M., Machín, E., & Reichard, M. (2019). Species coexistence and

628 sex ratio dynamics in annual fish assemblages in the lower Río Uruguay basin

629 *Environmental Biology of Fish*. DOI: 10.1007/s10641-019-00854-x

630 García, G., Gutiérrez, V., Vergara, J., Calviño, P., Duarte, A., & Loureiro, M. (2012).

631 Patterns of population differentiation in annual killifishes from the Paraná-

632 Uruguay-La Plata Basin: The role of vicariance and dispersal. *Journal of*

633 *Biogeography*, 39(9), 1707–1719. DOI: 10.1111/j.1365-2699.2012.02722.x

634 Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A

635 framework for community interactions under climate change. *Trends in Ecology*

636 *and Evolution*, 25(6), 325–331. DOI: 10.1016/j.tree.2010.03.002

637 Hassall,C., Billington, J., & Sherratt, T. N. (2019). Climate-induced phenological

638 shifts in a Batesian mimicry complex. *Proceedings of the National Academy of*

639 *Sciences*, 116(3), 929-933. DOI: 10.1073/pnas.1813367115

640 Hegg, J. C., Kennedy, B. P., Chittaro, P. M., & Zabel, R. W. (2013). Spatial

641 structuring of an evolving life-history strategy under altered environmental

642 conditions. *Oecologia*, 172(4), 1017–1029. DOI: 10.1007/s00442-012-2564-9

643 Hilbe, J. M. (2014). Bayesian Count Models. *Wiley StatsRef: Statistics Reference*

644 *Online*, 1-13. DOI: 10.1002/9781118445112.stat07963

645 Hsu, C. Y., & Chiu, Y. C. (2009). Ambient temperature influences aging in an annual

646 fish (*Nothobranchius rachovii*). *Aging cell*, 8(6), 726-737.

647 Kordas, R. L., Harley, C. D., & O'Connor, M. I. (2011). Community ecology in a

648 warming world: the influence of temperature on interspecific interactions in marine

649   systems. *Journal of Experimental Marine Biology and Ecology*, 400(1-2), 218-226.

650   DOI: 10.1016/j.jembe.2011.02.029

651 Lanés, L. E. K., Godoy, R. S., Maltchik, L., Polačik, M., Blažek, R., Vrtílek, M.,

652   Reichard, M. (2016). Seasonal dynamics in community structure, abundance, body

653   size and sex ratio in two species of Neotropical annual fishes. *Journal of Fish*

654   *Biology*, 89, 2345-2364.

655 Laufer, G., Arim, M., Loureiro, M., Piñeiro-Guerra, J. M., Clavijo-Baquet, S., &

656   Fagúndez, C. (2009). Diet of four annual killifishes: an intra and interspecific

657   comparison. *Neotropical Ichthyology* 7, 77-86.

658 Levels P. J., & Denucé, J. M. (1988). Intrinsic variability in the frequency of

659   embryonic diapauses of the annual fish *Nothobranchius korthausae*, regulated by

660   light: dark cycle and temperature. *Environmental Biology of Fishes* 22, 211–223.

661 Liu, R. K., & Walford, R. L. (1966). Increased growth and life-span with lowered

662   ambient temperature in the annual fish, *Cynolebias adloffi*. *Nature*, 212(5067),

663   1277.

664 Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D.

665   (2009). The velocity of climate change. *Nature*, 462, 1052-1055. DOI:

666   10.1038/nature08649

667 Loureiro, M., de Sá, R., Serra, W. S., Alonso, F, Lanés, L. E. K., Volcan, M. V., …

668   Garcia, G. (2018). Review of the family Rivulidae (Cyprinodontiformes,

669   Aplocheiloidei) and a molecular and morphological phylogeny of the annual fish

670   genus *Austrolebias* Costa 1998. *Neotropical Ichthyology*, 16(3). DOI:

671   10.1590/1982-0224-20180007

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

673   *Ecology & Evolution*, *19*(2), 94-100.

674   Mathias, A., & Chesson, P. (2013). Coexistence and evolutionary dynamics mediated

675   by seasonal environmental variation in annual plant communities. *Theoretical*

676   *Population Biology*, 84(1), 56–71. DOI: 10.1016/j.tpb.2012.11.009

677   Nylin, S., & Gotthard, K. (1998). Plasticity in life-history traits. *Annual review of*

678   *entomology*, 43(1), 63-83.

679   Paine, R. T. (1966). Food web complexity and species diversity. *The American*

680   *Naturalist*, 100(910), 65-75.

681   Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change.

682   *Annual Review of Ecology, Evolution, and Systematics*, 37(1), 637–669. DOI:

683   10.1146/annurev.ecolsys.37.091305.110100

684   Passos, C., Tassino, B., Reyes, F., & Rosenthal, G. G. (2014). Seasonal variation in

685   female mate choice and operational sex ratio in wild populations of an annual fish,

686   *Austrolebias reicherti*. *PLoS ONE*, 9(7). DOI: 10.1371/journal.pone.0101649

687   Podrabsky, J. E., Carpenter, J. F., & Hand, S. C. (2001). Survival of water stress in

688   annual fish embryos: dehydration avoidance and egg envelope amyloid fibers.

689   *American Journal of Physiology-Regulatory, Integrative and Comparative*

690   *Physiology*, 280(1), R123-R131.

691   Podrabsky, J. E., Garrett I. D. F., & Kohl, Z. F. (2010a). Alternative developmental

692   pathways associated with diapause regulated by temperature and maternal

693   influences in embryos of the annual killifish *Austrofundulus limnaeus*. *Journal of*

694   *Experimental Biology*, 213(19), 3280–3288. DOI: 10.1242/jeb.045906

695   Podrabsky, J. E., & Hand, S. C. (1999). The bioenergetics of embryonic diapause in

696   an annual killifish, *Austrofundulus limnaeus*. *Journal of Experimental Biology*,

697   202(19), 2567-2580.

698 Podrabsky, J. E., Hrbek, T., & Hand, S. C. (1997). Physical and chemical

699 characteristics of ephemeral pond habitats in the Maracaibo basin and Llanos

700 region of Venezuela. *Hydrobiologia*, 362(1-3), 67-77.

701 Podrabsky, J. E., Tingaud-Sequeira, A., & Cerdá, J. (2010b). Metabolic dormancy and

702 responses to environmental desiccation in fish embryos. In: Lubzens, E, J Cerdá,

703 M Clark (Eds), *Dormancy and resistance in harsh environments*. Berlin,

704 Heidelberg, Springer. pp.: 203-226.

705 Polačik, M., & Podrabsky, J. E. (2015). Temporary environments. In: Riesch, R.,

706 Tobler, M. & Plath, M. (Eds), *Extremophile fishes*. New York, Springer. pp.: 217–

707 245.

708 Polačik, M, & Reichard, M. (2010). Diet overlap among three sympatric African

709 annual killifish species *Nothobranchius* spp. from Mozambique. Journal of Fish

710 Biology, 77(3), 754–768. DOI: 10.1111/j.1095-8649.2010.02717.x

711 Polačik, M., Reichard, M., & Vrtílek, M. (2018). Local variation in embryo

712 development rate in annual fish. *Journal of Fish Biology*, 92, 1359-1370.

713 Polačik, M., Smith, C., Reichard, M. (2017). Maternal source of variability in the

714 embryo development of an annual killifish. *Journal of Evolutionary Biology*, 30,

715 738-749. DOI:10.1111/jeb.13038

716 R Core Team (2018). R: A language and environment for statistical computing.

717 Vienna, Austria: R Foundation for Statistical Computing. (http://www. R-

718 project.org/).

719 Rafferty, N. E., Caradonna, P. J., & Bronstein, J. L. (2015). Phenological shifts and

720 the fate of mutualisms. *Oikos*, 124(1), 14–21. DOI: 10.1111/oik.01523

721 Rafferty, N. E., & Ives, A. R. (2011). Effects of experimental shifts in flowering

722 phenology on plant-pollinator interactions. *Ecology Letters*, 14(1), 69–74.

723   Reichard, M. (2016). The evolutionary ecology of African annual fishes. In: Berois,

724   N, García, G, & de Sá, R (Eds). *Annual Fishes: Life History Strategy, Diversity,*

725   *and Evolution*. Boca Ratón, CRC Press. pp.: 133-158.

726   Reichard, M., & Polačik, M. (2019). *Nothobranchius furzeri*, an 'instant' fish from an

727   ephemeral habitat. *eLife*, 8, e41548.

728   Rollinson, C. R., Kaye, M. W., & Canham, C. D. (2016). Interspecific variation in

729   growth responses to climate and competition of five eastern tree species. *Ecology,*

730   *97*(4), 1003-1011.

731   Rohlf, F.J. (2009). tpsDig2, Version 2.1. State University of New York, Stony Brook.

732   Rue, H., Riebler, A., Sørbye, S. H., Illian, J. B., Simpson, D. P., & Lindgren, F. K.

733   (2017). Bayesian computing with INLA: a review. *Annual Review of Statistics and*

734   *its Application*, 4, 395-421.

735   Sæther, B. E., & Bakke, Ø. (2000). Avian life history variation and contribution of

736   demographic traits to the population growth rate. *Ecology*, 81(3), 642-653.

737   Stearns, S. C. (1992). *The evolution of life histories*. New York, Oxford University

738   Press.

739   Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J.,

740   Collingham, Y. C.,   … Williams, S. E. (2004). Extinction risk from climate

741   change. *Nature*, 427(6970), 145.

742   Trenberth, K. E. (2011). Changes in precipitation with climate change. *Climate*

743   *Research*, 47, 123–138. DOI: 10.3354/cr00953

744   Valenzano, D. R., Terzibasi, E., Cattaneo, A., Domenici, L., & Cellerino, A. (2006).

745   Temperature affects longevity and age related locomotor and cognitive decay in

746   the short lived fish *Nothobranchius furzeri*. *Aging cell*, 5(3), 275-278.

747   Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M. B., Balaguer, L., Benito‑

748   Garzón, M., … Zavala, M. A. (2014). The effects of phenotypic plasticity and local

749   adaptation on forecasts of species range shifts under climate change. *Ecology*

750   *Letters*, 17(11), 1351-1364.

751   Varpe, Ø. (2017). Life History Adaptations to Seasonality. *Integrative and*

752   *Comparative Biology*, 57(5), 943–960. DOI:10.1093/icb/icx123.

753   Volcan, M. V., Fonseca, A. P. D., Figueiredo, M. R. C., Sampaio, L. A., & Robaldo,

754   R. B. (2012). Effect of temperature on growth of the threatened annual fish

755   *Austrolebias nigrofasciatus* Costa &Cheffe 2001. *Biota Neotropica*, 12(4), 68-73.

756   Volcan, M. V., Gonçalves, Â. C., Lanés, L. E. K., & Guadagnin, D. L. (2016). Annual

757   fishes (Rivulidae) from Southern Brazil: A broad-scale assessment of their

758   diversity and conservation. In: Berois, N., Garcia, G., de Sa, R. (Eds.) *Annual*

759   *fishes: Life history strategy, diversity, and evolution.* Boca Ratón, CRC Press. pp.:

760   185-206.

761   Volcan, M. V., & Lanés, L. E. K. (2018). Brazilian killifishes risk extinction. *Science*,

762   DOI: 10.1126/science.aau5930

763   Walford, R. L., & Liu, R, K. (1965). Husbandry, life span, and growth rate of the

764   annual fish, *Cynolebias adloffi* E. Ahl. *Experimental Gerontology*, 1(2), 161-168.

765   Walther G. R., Post, E. Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C.,

766   Fromentin, J. M., Hoegh-Guldbergs, O., & Bairlein, F. (2002). Ecological

767   responses to recent climate change. *Nature*, 416, 389-395.

768   Witze, A. (2018). Why extreme rains are getting worse. *Nature*, 563, 458–460. DOI:

769   10.1038/d41586-018-07447-1

770 Wood, S. & Scheipl, F. (2017). gamm4: Generalized Additive Mixed Models using

771 'mgcv' and 'lme4'. *R package version 0.2-5*, https://CRAN.R-

772 project.org/package=gamm4.

773 Wootton R. J., & Smith, C. (2015). *Reproductive biology of teleost fishes*. Oxford,

774 Wiley.

775 Zebral, Y. D., Lansini, L. R., Costa, P. G., Roza, M., Bianchini, A., & Robaldo, R. B.

776 (2018). A glyphosate-based herbicide reduces fertility, embryonic upper thermal

777 tolerance and alters embryonic diapause of the threatened annual fish *Austrolebias*

778 *nigrofasciatus*. *Chemosphere*, 196, 260-269.

779 Zuur, A. F., & Ieno, E. N. (2016). A protocol for conducting and presenting results of

780 regression‐type analyses. *Methods in Ecology and Evolution*, 7, 636-645.

781 Zuur, A. F., Saveliev, A. A., & Ieno, E. N. (2014). *A beginner's guide to generalised*

782 *additive mixed models with R*. Newburgh, Highland Statistics Ltd.

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786 **Table 1.** Mean estimates, their standard errors (SE) and statistical significance for

787 gonad mass in *A. bellottii* as a function of coexistence with *A. nigripinnis*, body size

788 (TL, log-transformed) and their interaction, modelled using a zero-altered model with

789 pool identity included as a random term.

Parameter	(a) Occurrence model				(b) Frequency model			
	Estimate	SE	z	P	Estimate	SE	z	P
Intercept	-45.55	10.82	-4.21	<0.001	-9.91	0.44	-22.71	<0.001
Coexistence	-51.95	33.75	-1.54	0.124	-0.80	0.69	-1.15	0.254
logTL	32.45	7.68	4.23	<0.001	5.44	0.29	18.78	<0.001
Coexist:TL	36.65	23.91	1.53	0.125	0.51	0.46	1.13	0.264

790

791

792 **Table 2.** Posterior mean estimates of *A. bellottii* TL modelled using a gamma random

793 walk trend model fitted using INLA. CrI is the 95% Bayesian credible interval.

794 Credible intervals that do not contain zero indicate a statistically important difference.

795 *Sex* is mature fish sex. *Cohort* is the cohort of fish to which an individual belonged.

796 *Area* is the surface area of the pool in which fish were captured.

797

Model parameter	Posterior mean	Lower CrI	Upper CrI
Intercept	1.077	0.989	1.164
Sex(male)	0.119	0.106	0.132
Cohort(second)	0.236	0.201	0.271
Area	-0.008	-0.024	0.007

798

799

800   **Table 3.** Posterior mean estimates for gonad mass in *A. bellottii* as a function of cohort,

801   age and pool area, modelled using a zero-altered gamma (ZAG) model with pool

802   included as a random term. CrI is the 95% Bayesian credible interval. Credible intervals

803   that do not contain zero in bold to indicate statistical importance.

Parameter	(a) Occurrence model			(b) Frequency model		
	Posterior mean	Lower CrI	Upper CrI	Posterior mean	Lower CrI	Upper CrI
Intercept	**1.47**	**0.15**	**2.80**	**3.08**	**2.70**	**3.43**
Cohort(second)	**2.11**	**0.43**	**3.97**	**1.37**	**0.84**	**1.93**
Age	**3.83**	**2.83**	**4.95**	**0.86**	**0.75**	**0.99**
Area	-0.51	-1.29	0.21	**0.27**	**0.11**	**0.44**

804

805

Figure Captions

807 **Figure 1.** Location of the study area (A), with individual pools indicated (B).

808 Symbols for individual pools designate presence of a single cohort that either survived

809 the entire season (open symbol) or perished when the pool desiccated in mid-winter

810 (grey symbol), and the presence of the first and second cohort (black symbol). Pools

811 with *A. bellottii* and *A. nigripinnis* are marked by triangles and pools without *A.*

812 *nigripinnis* are indicated by circles. Note that in two pools, the first cohort survived

813 despite apparent desiccation.

814
815 **Figure 2.** Growth trajectories of *A. bellottii* males (A) and females (B) in pools

816 without *A. nigripinnis* (blue diamonds) or coexisting with *A. nigripinnis* (red

817 triangles). Individual body size measurements are indicated (TL, in cm), along with

818 GAMM-fitted curves with separate smoothers for presence/absence of *A. nigripinnis*.

819

820 **Figure 3.** Water temperature experienced by the first (grey) and second (black) cohort

821 of *A. bellottii* measured *in situ* using dataloggers. Daily mean values are presented.

822 Bars indicate hatching period for each cohort. Note that values experienced by the

823 first and second cohort overlap and values experienced by adults from the first cohort

824 from the age of 110 days are the same as those experienced by the second cohort from

825 day 0.

826

827 **Figure 4.** Growth trajectories of the first (blue circles) and second (red triangles)

828 cohorts of *A. bellottii* males (A) and females (B) and *A. nigripinnis* males (C) and

829   females (D). Individual body size measurements are indicated (TL, in cm), along with

830   GAMM-fitted curves with separate smoothers for each cohort.

831

832   **Figure 5.** Specific growth rates (SGR) of the first (blue circles) and second (red

833   triangles) cohort of *A*. *bellottii* (both sexes pooled). Note that formal analysis

834   compared only SGRs until Time 7 to avoid bias from unequal lifespan between the

835   two cohorts.

836

837   **Supporting Information Table S1**. Sample size for each pool, species, sex, and

838   sampling event.

839

840   **Supporting Information Figure S1**. Precipitation and temperature data for the study

841   area (Villa Soriano, Uruguay) comparing the year 2015 with 10 years database. Data

842   were provided by National Meteorology Institute, INUMET.