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**Trade-offs between accuracy and interpretability in von Bertalanffy
random-effects models of growth**

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Abstract

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24 Better understanding of variation in growth will always be an important problem in ecology,
25 since variation in growth can have substantial consequences for ecological and evolutionary
26 dynamics. Individual variation in growth can arise from a variety of processes; for example,
27 individuals within a population vary in their intrinsic metabolic rates and behavioral traits, which
28 may influence their foraging dynamics and access to resources. However, when adopting a
29 growth model, we face trade-offs between model complexity, biological interpretability of
30 parameters, and goodness of fit.

31 We explore how different formulations of the von Bertalanffy Growth Function (vBGF)
32 with individual random effects and environmental predictors affect these trade-offs. In the vBGF,
33 the growth of an organism results from a dynamic balance between anabolic and catabolic
34 processes. We start from a formulation of the vBGF that models the anabolic coefficient (q) as a
35 function of the catabolic coefficient (k), a coefficient related to the properties of the
36 environment (γ) and a parameter that determines the relative importance of behavior and
37 environment in determining growth (ψ). We treat the vBGF parameters as a function of
38 individual random effects and environmental variables. We use simulations to show how
39 different functional forms and individual or group variability in the growth function's parameters
40 provide a very flexible description of growth trajectories. We then consider a case study of two
41 fish populations of *Salmo marmoratus* and *Salmo trutta* to test the goodness of fit and predictive
42 power of the models, along with the biological interpretability of vBGF's parameters when using
43 different model formulations.

44 The best models, according to AIC, included individual variability in both k and γ and
45 cohort as predictor of growth trajectories, and are consistent with the hypothesis that habitat
46 selection is more important than behavioral and metabolic traits in determining lifetime growth
47 trajectories of the two fish species. Model predictions of individual growth trajectories were
48 largely more accurate than predictions based on mean size-at-age of fish. Our method shares
49 information across individuals, and thus, for both the marble and brown trout populations
50 investigated, allows using a single measurement early in the life of individual fish or cohort to
51 obtain accurate predictions of lifetime individual or cohort size-at-age.

52 **Keywords:** von Bertalanffy growth function; Model predictions; Marble trout; Brown trout;
53 Longitudinal data.

54 **1 Introduction**

55 Understanding individual growth will always be an important biological problem, as
56 survival, sexual maturity, reproductive success, movement and migration are commonly related
57 to growth and body size (Peters 1983). Thus, variation in growth can have substantial
58 consequences for ecological and evolutionary dynamics (Lomnicki 1988, Pelletier et al. 2007,
59 Coulson et al. 2010).

60 Experimental and observational studies provide information on growth throughout an
61 individual's lifetime or at specific life stages. However, a series of data points on size-at-age is
62 difficult to interpret without reference to a model of growth, but non-linear growth models allow
63 us to condense the information contained in such a data series into a few parameters. In some
64 growth models, those parameters are biologically interpretable, i.e. they represent or summarize
65 the most relevant biological processes and environmental factors determining variation in growth
66 (West et al. 2004), while parameters of other growth models do not have a clear mechanistic
67 interpretation and are best considered as curve-fitting parameters (Text A1).

68 Growth models have multiple applications in ecology and evolutionary biology. For
69 instance, when managing human intervention in natural populations, we may be interested in:

- 70 • Understanding how growth rates and size-at-age vary in time and space depending on
71 environmental conditions within- and among-populations of the same species (Vincenzi et al.
72 2014b);
- 73 • Inferring life-history strategies, i.e. trade-offs between allocation of resources to
74 competing physiological functions such as growth, maintenance, and reproduction throughout
75 the lifetime (Roff 2007); or
- 76 • Estimating heritability of growth and size-at-age (Carlson and Seamons 2008).

77 Another potential application of growth models (e.g. for fisheries management) is the
78 prediction of lifetime growth trajectories of individuals or group of individuals (e.g. year-of-birth
79 cohort, same-sex individuals) from observations at early life stages. Growth models have been
80 mostly used for describing or interpreting population and individual processes, but have seldom
81 been used for predictive purposes in ecology (Peters 1991), although an ample literature exists

82 for health applications in humans (Berkey 1982, Radhakrishna Rao 1987, Shohoji et al. 1991,
83 Roland et al. 2011).

84 For both basic and applied ecological goals, the choice of the growth model is often critical.
85 Across growth models, we often face trade-offs between model complexity, biological
86 interpretability of model parameters, ease of parameter estimation, and model accuracy, i.e. the
87 combination of goodness of fit and predictive power. These trade-offs are commonly faced in
88 other ecological contexts (Ludwig and Walters 1985, Adkison 2009). For instance, Ward et al.
89 (2014) tested the predictive performance of short-term forecasting models of population
90 abundance of varying complexity. They found that more complex parametric and non-parametric
91 models often performed worse than simpler models, which simply treated the most recent
92 observation as the forecast. In their case, the estimation of even a small number of parameters
93 imposed a high cost while providing little benefit for short-term forecasting of species without
94 obvious cyclic dynamics. However, when a signal of cyclic dynamics was clearly identifiable,
95 more complex models were able to extract meaningful patterns from data and more accurately
96 predict future abundances. Thus, the complexity of the best predictive model will be determined
97 by the ecological situation.

98 A broad range of models describing the variation in size of organisms throughout their
99 lifetime have been proposed (von Bertalanffy 1957, Lester et al. 2004, Quince et al. 2008,
100 Kimura 2008, Kooijman 2009, Omori et al. 2009, Russo et al. 2009), with varying degrees of
101 model complexity, biological interpretability of parameters, and data requirements for parameter
102 estimation. For some growth models, parameters may or may not be biologically interpretable
103 depending on model formulation. For instance, the parameters of the widely used von
104 Bertalanffy growth function (vBGF, von Bertalanffy 1957) to model growth of fish may be
105 considered either curve fitting parameters with no biological interpretation (i.e. providing just a
106 phenomenological description of growth) or parameters that describe how anabolic and catabolic
107 processes govern the growth of the organism (i.e. mechanistic description); see Mangel (2006).
108 The classic vBGF has 3 parameters: asymptotic size, growth rate, and theoretical age at which
109 size is equal to 0 (or size at age 0 in an equivalent formulation). In the original mechanistic
110 formulation of von Bertalanffy, asymptotic size results from the relationship between
111 environmental conditions and behavioral traits, and the growth coefficient is closely related to
112 metabolic rates and behavioral traits (i.e. the same physiological processes affect both growth

113 and asymptotic size). However, in the literature asymptotic size and growth rate are commonly
114 treated as independent parameters with no connection to physiological functions, thus becoming
115 a phenomenological description of growth.

116 In the vast majority of applications of growth models, parameters are estimated at the
117 population level but interpreted as those of an average individual in the population. This
118 approach fails to take into account the substantial variation in growth observed within
119 populations, and severely limits the breadth and scope of the models (Sainsbury 1980, Siegfried
120 and Sansó 2006, Vincenzi et al. 2014b). Individual variation in growth can arise from a variety
121 of processes. For example, individuals within a population vary in their intrinsic metabolic rates
122 and behavioral traits (e.g. aggressiveness or territoriality) (Rosenfeld et al. 2014), which may
123 have consequences for their foraging dynamics and access to resources. Realized growth is a
124 combination of an individual's intrinsic growth potential, environmental conditions, intra- and
125 interspecific competition, and stochastic events. For these reasons, the estimation of individual
126 variation in growth is biologically and computationally difficult, and requires longitudinal data
127 (Shelton and Mangel 2012). Random-effects models provide an intuitive framework for
128 estimating heterogeneity of growth within- and among-populations along with individual growth
129 trajectories (Sainsbury 1980, Eveson et al. 2007, Sigourney et al. 2012).

130 Here, we explore how different formulations of the widely used vBGF with individual
131 random effects offer different degrees of biological interpretability of model parameters,
132 goodness of fit, and prediction of future growth trajectories or unobserved growth realizations.
133 We start from the model that Snover et al. (2005) developed for management of coho salmon
134 *Oncorhynchus kisutch*, which treats the anabolic factor in the vBGF as the product of the
135 catabolic factor and a factor related to the properties of the environment, and show how
136 correlation among parameter estimates arises and how different functional forms and individual
137 or group variability in the growth function's parameters provide a very flexible description of
138 growth trajectories. However, flexibility comes at a cost, since it potentially reduces the
139 biological interpretability of the parameters of the vBGF.

140 We use simulated data and test whether the same growth trajectories can be obtained using
141 different formulations and parameter combinations of the vBGF. We investigate the correlation
142 between parameter estimates, as the sign and strength of the correlation give insights on life-

143 history strategies (Vincenzi et al. 2014b). We use one population of marble trout (*Salmo*
144 *marmoratus*) and one population of brown trout (*Salmo trutta* L.) living in streams located in
145 Western Slovenia (Zakojska and Upper Volaja, respectively) as model systems for the fitting and
146 application of the growth model.

147 Marble trout is a resident salmonid endemic in Northern Italy and Slovenia that is at risk of
148 extinction due to hybridization with brown trout (Vincenzi et al. 2008) and massive mortalities
149 associated with catastrophic flood events, whose frequency is increasing (Vincenzi et al. 2014a).
150 Brown trout was introduced in Upper Volaja in the 1920s, with no additional stocking of fish
151 after the introduction. Growth patterns and size-at-age in salmonids contribute to determine
152 survival (Woodson et al. 2013), sexual maturity and reproductive success (Jonsson and Jonsson
153 2011), so that having a better understanding of growth has important implications for our
154 understanding of the ecology of the two species, their population dynamics, the evolution of life-
155 history traits, and for the effective applications of conservation measures. For those populations,
156 we test the goodness of fit of the models along with the empirical correlation between parameter
157 estimates. Then, we test the ability of the models to predict future or unobserved size-at-age data.
158 We finally discuss the biological interpretation of the vBGF's parameters, which are modeled as
159 function of individual random effects and environmental predictors.

160 **2 Material and methods**

161 **2.1 Growth model**

162 We use an extension of the model due to von Bertalanffy (vBGF, von Bertalanffy 1957,
163 Essington et al. 2001, Mangel 2006), which has been used to model the growth of organisms
164 across a wide range of taxa (Kingsley 1979, Zullinger and Ricklefs 1984, Shine and Charnov
165 1992, Starck and Ricklefs 1998, Frisk et al. 2001, Lester et al. 2004, Tjørve and Tjørve 2010).

166 We start with a description of the standard vBGF and we then follow with a formulation of
167 the vBGF that allows for a description of the growth process in terms of interaction between
168 individual behavior and properties of the environment.

169 **2.1.1 The standard von Bertalanffy growth function**

170 In the vBGF, the growth of an organism results from a dynamic balance between anabolic
171 and catabolic processes (von Bertalanffy 1957), where anabolic processes are those leading

172 to tissue growth, differentiation of cells, and increase in body size, and catabolic processes are
 173 those involving the breakdown of complex molecules and the release of energy. If $W(t)$ denotes
 174 mass at time t , the assumption of the vBGF is that anabolic factors are proportional to surface
 175 area, which scales as $W(t)^{2/3}$, and that catabolic factors are proportional to mass. If a and b
 176 denote these proportionality parameters, then the rate of change of mass is

$$177 \quad \frac{dW}{dt} = aW(t)^{2/3} - bW(t) \quad (2.1)$$

178 If we further assume that mass and length, $L(t)$, are related by $W(t) = \rho L(t)^3$ with ρ
 179 corresponding to mass per unit volume, then

$$180 \quad \frac{dL}{dt} = q - kL \quad (2.2)$$

181 where $q = a/3\rho$ and $k = b/3\rho$. In this parameterization, q is a coefficient of anabolism.
 182 The coefficient of catabolism, k , is commonly known as the von Bertalanffy growth coefficient
 183 and has the units of t^{-1} . The coefficient q , with unit $size \cdot t^{-1}$, is proportional to the amount of
 184 resources available to an individual and will vary with environmental conditions and individual
 185 behavior. The asymptotic size (i.e. obtained by setting $q - kL$ equal to 0 in Eq. 2.2) is $L_\infty = \frac{q}{k}$
 186 and if $L(0) = L_0$ is size at age 0, we can readily solve the linear differential equation 2.2 by the
 187 method of the integrating factor. Two forms of the solution are

$$188 \quad L(t) = L_\infty (1 - e^{-kt}) + L_0 e^{-kt} \quad (2.3)$$

189 and

$$190 \quad L(t) = L_\infty (1 - e^{-k(t-t_0)}) \quad (2.4)$$

191 where t_0 is the hypothetical age at which length is equal to 0.

192 The vBGF model in Eq. 2.4 has 3 parameters: L_∞ , k , t_0 (in addition to the residual variance
 193 when parameter values are estimated), which are usually estimated at the population or group
 194 (e.g. cohort, sex) level. L_∞ is commonly treated as an independent parameter (i.e. not an explicit

195 function of k , although a negative correlation between parameter estimates often emerges due to
196 the presence of ridges in the likelihood surface, in particular when length-at-age data for older
197 ages are relatively few or missing, see Vincenzi et al. 2014b) and the vBGF has often been used
198 as a phenomenological and not mechanistic description of the growth process (although see
199 Essington et al. (2001) and Temming & Herrmann (2009) for estimating consumption rates from
200 vBGF parameter values). In this paper, we will not make explicit reference to L_∞ , as it does not
201 provide any insights on the behavioral and physiological processes governing growth.

202 **2.1.2 Model with individual variation in parameters of anabolism and catabolism**

203 There are biological reasons for k (the coefficient of catabolism) and q (the coefficient of
204 anabolism) to be linked (Shelton and Mangel 2012, Shelton et al. 2013). Therefore, we turn to a
205 model that combines individual and environmental variation and allows dependence between k
206 and q along with individual variation, i.e. k and q are defined and estimated at the individual
207 level. Since q is the coefficient of anabolism, it should be closely linked to bottom-up factors in
208 the environment, such as food conditions (Mangel 2006). By letting q vary across individuals (q_i), we assume that “realized anabolism” may vary across individuals. The parameter k_i
209 determines how metabolic rates scale with the size of individual i and thus relates to an
210 individual’s phenotypic capacity for growth. Snover et al. (2005, 2006) assume that k_i
211 combines physiological and behavioral traits that determine individual activity and thus
212 potentially affect the ability of an individual to obtain resources from the environment, although
213 with a trade-off with energy expenditure. Thus, the “anabolic” conditions may be different for
214 individuals and they may depend on k_i as well as some properties of the environment. Under
215 these assumptions, we model q_i as a function of k_i , γ_i , and a parameter ψ constrained
216 between 0 and 1 that determines the degree to which q_i depends on environmental (represented
217 by γ_i) versus behavioral (represented by k_i) factors, and set

$$219 \quad q_i = \gamma_i k_i^\psi \quad (2.5)$$

220 With the formulation in Eq. 2.5, ψ is the result of the interaction of the environment and
221 the foraging characteristics of the species, and may depend for instance on patchiness of

222 resources, fragmentation of the habitat, movement range of individuals. Units of γ depend on the
223 value of ψ : when $\psi = 0$, γ has the units of q ($size \cdot t^{-1}$); when $\psi = 1$, γ has the units of size,
224 while units are fractal when $0 < \psi < 1$.

225 With Eq. 2.5, the expected length of individual i at age t is

$$226 \quad L_i(t) = \gamma_i k_i^{(\psi-1)} (1 - e^{-k_i(t-t_0)}) \quad (2.6)$$

227 Eq. (2.6) is the formula describing length-at-age for individual i in group j (e.g. sex,
228 cohort) that we will use in this work.

229 ***The case with γ common and k varying among individuals***

230 The case with γ common and k varying among individuals has been investigated in Snover
231 et al. (2005, 2006), and Shelton & Mangel (2012). In this case, parameters have a clear
232 biological interpretation when (a) $\psi = 0$, (b) $\psi = 1$, and (c) ψ between 0 and 1.

233 When (a) $\psi = 0$, k_i has no effect on an individual's success at obtaining resources from
234 the environment. Therefore, individuals with large k_i have lower realized growth increments,
235 since higher activity comes at a higher energetic cost. When (b) $\psi = 1$, individuals with large k_i
236 (i.e. aggressive and/or highly active individuals) have greatly increased access to resources, and
237 therefore experience faster length-specific growth. For (c) values of ψ between 0 and 1, the
238 relative growth rate for each individuals with different k_i will change with an individual's
239 length. Individuals with large k_i will grow faster at small lengths and individuals with small k_i
240 will grow faster at large size; the length or age at which individuals experience equivalent
241 growth and when growth trajectories cross depends on ψ .

242 ***The case with both γ and k varying among individuals***

243 We hypothesize that k_i and γ_i co-vary among individuals. This additional variability in γ_i
244 increases the complexity of the model by increasing the number of parameters to be estimated,
245 and allows for a greater flexibility of growth trajectories of individuals (Fig. 1). For instance,
246 while with a common γ between 0 and 1 and only k varying among individuals all growth

247 trajectories intersect at the same age, with both k_i and γ_i co-varying among individuals we
248 obtain a distribution of ages at which growth trajectories intersect.

249 However, a biological interpretation of the two parameters k_i and γ_i , and in particular of
250 ψ , becomes more challenging with respect to the case with only k_i varying among individuals.
251 In fact, we will show that the biological interpretation of ψ depends on the sign and strength of
252 the correlation between values of k_i and γ_i , and ψ may also be seen as a parameter giving
253 additional flexibility to the vBGF, rather than describing the relative importance of
254 environmental and behavioral factors in determining q_i .

255 As ψ is defined at the population level, but k_i and γ_i are allowed to vary among
256 individuals, we describe potential growth trajectories by first fixing ψ (i.e. the relative
257 importance of behavioral and environmental factors in determining anabolism) and explore how
258 growth trajectories may change with different strength and sign of correlation between values of
259 k_i and γ_i (Fig. 1).

260 When $\psi = 0$, the maintenance of size ranks through the lifetime of individuals and the mean
261 age at which growth trajectories cross decreases going from a negative to a positive correlation
262 between values of k_i and γ_i . In the limiting case of a correlation between values of k_i and γ_i
263 equal to 1, growth trajectories never cross throughout the lifetime of individuals for any variance
264 of k_i and γ_i (Figures S1 and S2). When $\psi = 0$, aggressive/more active individuals (larger k_i)
265 are always growing slower than less aggressive/active individuals. Thus, we may hypothesize
266 that the more active individuals are either expending more energy than less active individuals
267 without acquiring more resources, or are investing more energy on biological processes other
268 than growth.

269 On the other hand, when $\psi = 1$ (i.e. asymptotic size is not an explicit function of k), the
270 maintenance of size ranks (i.e. of size hierarchy) through an organism's lifetime and mean age at
271 which growth trajectories cross increases going from a negative to a positive correlation between
272 values of k_i and γ_i (Fig. 1). In the limiting case of a correlation between k_i and γ_i equal to 1,
273 growth trajectories never cross through organisms' lifetime (i.e. size ranks are always maintained
274 throughout the lifetime of individuals), thus aggressive and/or highly active individuals are

275 always able to obtain a higher share of resources (and invest them in growth). Thus, a similar
 276 pattern of growth at the population level emerges when $\psi = 0$ and values of k_i and γ_i are
 277 strongly negatively correlated or when $\psi = 1$ and values of k_i and γ_i are strongly positively
 278 correlated, but the biological and environmental processes leading to the emergence of similar
 279 growth trajectories are different. For values of ψ between 0 and 1, a rich variety of growth
 280 trajectories can be obtained depending on the correlation between values of k_i and γ_i as well as
 281 their variances (Fig. 1), although the biological interpretation of ψ is challenging with respect
 282 to the case of individual variability only for k , in particular with values of ψ far from either 0
 283 or 1.

284 2.2 Parameter estimation and individual variation

285 Formulations of the standard vBGF with individually varying parameters (L_∞ , k , t_0) have
 286 been proposed previously (Sainsbury 1980, Francis 1988, Wang and Thomas 1995, Laslett et al.
 287 2002, Pilling et al. 2002, Eveson et al. 2007, Sigourney et al. 2012). Here, we present a novel
 288 formulation of the vBGF (as described in Section 2.1) specific for longitudinal data where γ , k ,
 289 and t_0 are a function of shared predictor(s) (as explained below) and individual random effects.

290 We treat t_0 and ψ as population-level parameters (with no environmental predictors and no
 291 individual random effects), so that all individuals are assumed to share the same value. This
 292 improves the biological interpretation of the other parameters and helps with model fitting, as
 293 explained below. Since k and γ must be non-negative, we use a log-link function to facilitate
 294 parameter estimation and convergence of the model fitting procedure. For individual i in group j
 295 (e.g. sex, year-of-birth cohort) we thus set

$$296 \begin{cases} \log(k_{ij}) = \log(k_0) + \alpha_j x_i + \sigma_u u_{ij} \\ \log(\gamma_{ij}) = \log(\gamma_0) + \beta_j x_i + \sigma_v v_{ij} \\ t_0^{(\psi)} = t_0 \end{cases} \quad (2.7)$$

297 where u_{ij} and v_{ij} are the standardized individual random effects, σ_u and σ_v are the standard
 298 deviations of the statistical distributions of the random effects (which we take to have prior
 299 distributions that are normal, while the posterior distribution is not guaranteed to be normal due

300 to the non-linearity of the likelihood function), k_0 and γ_0 are population-level parameters, α_j
 301 and β_j are group-level parameters, and x_i has value of 1 if individual i is in group j and 0
 302 otherwise. The model with no predictors and no individual random effects contains only 4
 303 parameters (plus the residual variance), $\log(k_0), \log(\gamma_0), t_0, \psi$ i.e. parameters are estimated at the
 304 whole population level with no individual variation in growth. In the following, we report and
 305 interpret parameter estimates of k_0 and γ_0 on their natural scale, as this allows to directly
 306 comparing their estimates to published values.

307 We use the Automatic Differentiation Model Builder (ADMB) software to estimate the
 308 parameters of the growth models (Vincenzi et al. 2014b). ADMB is an open source statistical
 309 software package for fitting non-linear statistical models (Fournier et al. 2012, Bolker et al.
 310 2013) that is quickly becoming a standard tool for use in fisheries stock assessment and
 311 management. ADMB-RE (the random effects module of ADMB) has the ability to fit generic
 312 random-effects models using an Empirical Bayes approach that implements the Laplace
 313 approximation (Skaug and Fournier 2006). Empirical Bayes (EB) refers to a tradition in statistics
 314 where the fixed effects and variance (or standard deviation) of a random-effects model are
 315 estimated by maximum likelihood, while estimates of random effects are based on Bayes
 316 formula. Although traditionally random effects are predicted and fixed effects are estimated, we
 317 refer in this paper to estimates of k_i and γ_i . Model fitting in ADMB-RE automatically stops
 318 when the maximum gradient (i.e. the larger of the partial derivatives of the likelihood function
 319 with respect to model parameters) is $< 10^{-4}$ (appropriate with log-transformed model parameters).

320 The length of individual i in group j at age t is

$$321 \quad L_{ij}(t) = \gamma_j k_j^{(\psi-1)} (1 - e^{-k_j(t-t_0)}) + \varepsilon_{ij} \quad (2.8)$$

322 where ε_{ij} is normally-distributed with mean 0 and variance σ_ε^2 (estimated in the model-fitting
 323 procedure).

324 For simplicity, we do not explicitly introduce process stochasticity, so that the likelihood is
 325 (Hilborn and Mangel 1997)

326
$$\prod_{j=1}^J \prod_{i=1}^{n_j} \prod_{l=1}^{m_{ij}} \frac{1}{\sqrt{2\pi\sigma_\epsilon}} \exp\left(-\frac{\left(L_{ijl} - L(t_{ijl}; \gamma_{ij}, k_{ij}, t_0^{(ij)}, \psi)\right)^2}{2\sigma_\epsilon^2}\right) \quad (2.9)$$

327 where n_j is the number of individuals in group j , J is the number of groups, m_{ij} is the number of
 328 observations from individual i of group j , l is an index that run over these observations. Further,
 329 the observed length measurements for individual i in group j are denoted by L_{ijl} , while t_{ijl} is the
 330 age of the individual when the l -th measurement is made. In the following, we will simply use k_i
 331 and γ_i for the individual-level parameters.

332 Note that Eq. 2.9 is only the likelihood for the observation part of the model. To obtain the
 333 likelihood that is used for parameter estimation it is necessary to include the contributions from
 334 the random effects, and to integrate the joint likelihood with respect to the random effects
 335 (Vincenzi et al. 2014b).

336 We give a description of model parameters, model assumptions and imposed parameter
 337 values or their empirical estimates/relationship in Table 1.

338 2.3 Case study

339 We use as model systems for fitting and application of the growth model one population of
 340 marble trout living in Zakojska stream and one population of brown trout living in Upper Volaja
 341 stream in the Western region of Slovenia (Vincenzi et al. 2012) (Fig. 2). The population of
 342 Zakojska was established in 1996 by stocking age-1 fish that were the progeny of parents from a
 343 relict genetically pure marble trout population (Crivelli et al. 2000). Fish hatched in Zakojska
 344 for the first time in 1998 and the 1998 cohort is the first included in the analysis. Upper Volaja
 345 was sampled for the first time in 2006 and the oldest cohort to be included in the analysis was
 346 born in year 2000. The two populations were sampled annually in June. Fish were collected by
 347 electrofishing and measured for length and weight to the nearest mm and g. If fish were caught
 348 for the first time - or if the tag had been lost - and they were longer than 110 mm they were
 349 tagged with Carlin tags (Carlin 1955) and age was determined by reading scales. Males and
 350 females in both marble and brown trout are morphologically indistinguishable at the time of
 351 sampling. The probability of capture at time t of a fish alive at time t was higher than 80%

352 (Vincenzi et al. 2008). Marble trout females reach sexual maturity when longer than 200 mm,
353 usually at age 3 or older, while age at first reproduction for brown trout in Upper Volaja occurs
354 at age 2 or older. The maximum observed age for fish born in the streams was 9 and 10 years in
355 Zakojska and Upper Volaja, respectively. The last sampling occasion included in the dataset was
356 June 2013. In Upper Volaja, the last cohort included was the one born in 2011. Due to a flood
357 that almost completely wiped out the population in 2007 (Vincenzi et al. 2012), there were no
358 fish born in Zakojska in 2008-2010. Also in Zakojska, the last cohort included was the one born
359 in 2011. Density of fish age-1 and older (number m^{-2}) was (mean \pm sd) 0.05 ± 0.04 in Zakojska
360 from 1998 to 2013 and 0.05 ± 0.05 in Upper Volaja from 2006 to 2013. In total, 1141 unique fish
361 were included in the Zakojska dataset and 1649 in the Upper Volaja dataset.

362 **2.4 Statistical analysis**

363 **2.4.1 Simulated data**

364 As this is the first time the model in Eq. (2.8) is proposed, we started by studying the
365 behavior of the model using simulated data. First, we tested whether the same growth trajectories
366 could be described using the parameter and growth functions in Eqs. 2.7 and 2.8 with different
367 values of Ψ from 0 to 1 with a step of 0.1 (Ψ is the set of ψ values we used). To do so, we first
368 simulated 400 (potentially) 10-year long unique growth trajectories with a true (i.e. data-
369 generating) Ψ (ψ_s) in Eq. 2.8 and for different scenarios with positive, negative or no
370 correlation (r_s) between the 400 pairs of k_i and γ_i . Specifically, we imposed a correlation
371 structure between normal distributions of individual random effects for k_i and γ_i (u_i and v_i ,
372 respectively), we randomly drew 400 (u_i, v_i) pairs from the joint probability distribution of
373 random effects, and then obtained 400 ($\log(k_i), \log(\gamma_i)$) pairs following Eq. (2.7). To simulate a
374 realistic empirical case, we used a mortality rate M and excluded one observation, on average,
375 per individual. We did not introduce group parameters to simulate individual growth trajectories
376 (i.e. $\alpha_j = \beta_j = 0$ in Eq. 2.7). Then, we fitted the model to the simulated growth trajectories by
377 fixing the value of Ψ (ψ_f) in Eq. 2.8. Due to the random sampling of u_i and v_i from the joint
378 probability distribution, we ran 10 random replicates for each combination of ψ_s , ψ_f , and r_s ,
379 and recorded the convergence of the model fitting procedure as determined by the maximum

380 gradient in ADMB-RE, average over replicates Mean Absolute Error (MAE) (i.e. mean absolute
381 difference between simulated length-at-age and length-at-age predicted by the fitted model) and
382 mean correlation between the 400 estimated pairs of k_i and γ_i (r_f) across replicates (\bar{r}_f) that
383 successfully converged. We did not compare data-generating parameter values and parameter
384 estimates as they can be meaningfully compared only when $\psi_s = \psi_f$. We also recorded how
385 many times over the 10 random replicates for each combination of ψ_s , ψ_f , and r_s the model
386 fitting procedure failed to converge. Convergence failure means that ADMB-RE was not able to
387 obtain a sufficiently small likelihood gradient, with the (default) criterion being 10^{-4} for all
388 parameters. The particular reason for lack of convergence may vary across simulation replicates,
389 and although it is not feasible to investigate each case in detail, it is good practice to keep track
390 of the number of cases in which convergence was not achieved.

391 ***2.4.2 Selection of the best growth model for Zakojska and Upper Volaja and prediction of*** 392 ***unobserved data***

393 We checked the maximum gradient component to ensure that a satisfactory convergence
394 was reached. Except for the case of non-linear regression explained further below, each model
395 we tested included individual random effects as in Eq. 2.7. Following Vincenzi et al. (2014b), we
396 introduced year-of-birth cohort as fixed categorical effects to test whether its inclusion as
397 predictor included model fitting to data for either population (α_j and β_j in Eq. 2.7). The model
398 may not be always not statistically identifiable, in that ψ can only sometimes be estimated
399 (Shelton and Mangel 2012). Thus, we fitted separately models with or without cohort as
400 predictors of γ_i , k_i or both with ψ from 0 to 1 with a step of 0.1. We used the Akaike
401 Information Criterion (Akaike 1974, Burnham and Anderson 2002) to select the best model. We
402 then investigated correlation between the estimates of k_i and γ_i at the individual level. We
403 tested whether the inclusion of individual random effects for both k_i and γ_i (thus increasing
404 model complexity) increased model accuracy with respect to models that include individual
405 random effects only for k_i (i.e. models in Shelton & Mangel 2012; Shelton et al. 2013). For the
406 latter model, in Eq. 2.8 we thus fixed $\sigma_v = 0$.

407 We tested whether vBGF models with random effects for both k_i and γ_i with different
408 values of ψ predicted substantially different mean cohort-specific growth trajectories. In
409 addition, we tested whether fitting non-linear least-squares regression with no random effects on
410 cohort-specific data (using the *nls* function in R (R Development Core Team 2011)) leads to
411 substantially different mean cohort-specific growth trajectories with respect to random-effect
412 models.

413 We tested the predictive ability of (a) the best overall vBGF model with individual variation
414 for both k and γ (where ψ_b is the value of ψ for the best model), as well as the models with (b)
415 $\psi = 0$ and (c) $\psi = 1$ for both populations. We also tested the predictive ability of the best
416 overall vBGF model with variation only for k . For each population, we: (i) randomly sampled
417 one third of fish that have been sampled more than 3 times throughout their lifetime (validation
418 sample); (ii) deleted from the data set all observations except the first one from each individual
419 fish in the validation sample; (iii) estimated the parameters of the vBGF for each individual
420 including those in the validation sample; and (iv) predicted the missing observations.

421 We compared the predictions of the vBGF to the predictions given by the mean
422 length-at-age of the cohort of the fish. We used MEA and R^2 with respect to the 1:1 line
423 observed data vs. predicted data as measures of predictive ability. The predictive abilities of the
424 vBGF models were tested using the same 10 random validation samples for each population.

425 **3 Results**

426 **3.1 Simulated data**

427 Model fitting with simulated data showed that when growth trajectories had a negative
428 correlation r_s between k_i and γ_i , the average correlation between k_i and γ_i across replicates
429 \bar{r}_f tended to remain negative in the area below the 1:1 line in the $\psi_s - \psi_f$ plane and around zero
430 or positive above the line (Fig. 3a). When growth trajectories were simulated starting from a
431 positive r_s , \bar{r}_f tended to remain close to 0 or slightly negative in the fitted models below the 1:1
432 line and mostly positive above the line (Fig. 3c). When r_s was equal to 0, the empirical
433 correlation between estimated k_i and γ_i in the fitted models tended to be around 0 for the

434 majority of combinations of ψ_s and ψ_f (Fig. 3b). Similar results were obtained when using
435 different variances of the individual random effects (Fig. A3 and A4).

436 The probability of convergence of the model fitting procedure varied across combinations of
437 ψ_s , ψ_f , and r_s . Although a clear pattern of probability of convergence did not emerge, the
438 model-fitting algorithm converged for most of the $\psi_s - \psi_f$ combinations and replicates (Fig. 3d-
439 f). The average of MAE across replicates was smaller than 2 mm (thus an almost perfect fit) in
440 more than 90% of the combinations of ψ_s and ψ_f .

441 3.2 Case study

442 Observed trajectories showed higher individual variation in growth and length at age in the
443 marble trout population of Zakojska than in the brown trout population of Upper Volaja (Fig. 2).

444 For the vBGF models without cohort as a predictor for either k_i and γ_i , the correlation
445 between k_i and γ_i was function of ψ (Fig. 4), and tended to shift from a negative to a positive
446 correlation with increasing values of ψ for both populations. In this case, for the population of
447 Upper Volaja the best model according to AIC had $\psi = 0.6$ (AIC = 23 855.4), while the model
448 with $\psi = 0$ had lower AIC than the model with $\psi = 1$ (23 951.4 vs. 24 059.2). For the
449 population of Zakojska the best model according to AIC had $\psi = 0.3$ (AIC = 17 387.8), while
450 the model with $\psi = 0$ had lower AIC than the model with $\psi = 1$ (17 395.9 vs. 17 445.1). The
451 joint distribution of ψ and sign and strength of the correlation between k_i and γ_i (Fig. 4)
452 suggested maintenance of size ranks throughout fish lifetime for both Zakojska and Upper
453 Volaja trout populations, with growth trajectories crossing on average after sexual maturity (Fig.
454 1). Every model predicted the observed data to high accuracy (Zakojska: range of MAE = 7.1-8.5
455 mm, range of $R^2 = 0.98$ -0.98; Upper Volaja: MAE = 3.7-5.0 mm, $R^2 = 0.97$ -0.98). Assuming a
456 lifespan of 10 years (i.e. predicting 10 years of length-at-age for each fish), growth trajectories
457 predicted using estimated parameters for models with different value of ψ (and without cohort
458 as predictor of either parameter) had similar mean age at crossing of growth trajectories and CV
459 of length at age 10, but substantially different number of trajectories crossing throughout the
460 lifetime of fish (Fig. 5).

461 For marble trout, the best model using AIC as model-selection criterion had cohort as
462 predictor both in k_i and γ_i and $\psi = 0.3$ (Table 2). For brown trout, the best model had cohort
463 as predictor for only γ_i and $\psi = 0.6$. For both Zakojska and Upper Volaja populations, the
464 models with individual random effects only in k_i performed far worse than the models with
465 individual random effects for both parameters (Table 2).

466 Cohort-specific models for marble trout and brown trout with cohort as predictor both in k_i
467 and γ_i provided essentially the same mean trajectories when ψ was equal to 1 and when ψ
468 was the one giving the smallest AIC (i.e. $\psi = 0.3$ for Zakojska and $\psi = 0.5$ for Upper Volaja)
469 (Fig. 6). Cohort-specific vBGF models with no random effects fitted with standard non-linear
470 least-squares regression predicted substantially greater length-at-age than random-effects
471 models for the marble trout population of Zakojska, while provided the same mean cohort-
472 specific growth trajectories as the random-effects models for the brown trout population of
473 Upper Volaja (Fig. 6).

474 **3.2.1 Prediction of unobserved length-at-age**

475 In the population of Upper Volaja and Zakojska, 132 and 63 fish were sampled more than 3
476 times during their lifetime, respectively. The vBGF model with both k and γ function of cohort,
477 individual random effects, and $\psi = 1$ provided consistently better prediction of the missing
478 observations than models with $\psi = 0$, ψ giving the best AIC value for models with both k and
479 γ function of cohort, and than prediction based on mean length-at-age of the respective cohort
480 (Table 3 and Figs. 7 and 8). The best model with individual variation only in k_i provided
481 substantially worse predictions than the best model with individual variation for both k_i and γ_i .

482 **4 Discussion**

483 Our formulation of the von Bertalanffy growth function balances biological details of the
484 growth process and model fitting, and thus provides a flexible and powerful framework for
485 estimating and understanding the role of abiotic and biotic factors in determining organisms'
486 growth. This unification is achieved by an ecological – rather than purely statistical – focus that

487 considers growth in terms of the behavior–environment interaction. Adding complexity in the
488 form of individual variability in both mechanistic parameters (k and γ) of our formulation of the
489 von Bertalanffy growth function increases model accuracy with respect to the model including
490 individual variability only in k , i.e. the parameter summarizing physiological and behavioral
491 traits that determine individual activity. We now discuss the results of our simulations, parameter
492 estimation and model selection using two fish populations as a case study, and their implications
493 for our understanding of the determinants of variation and for management and conservation.

494 **4.1 Relationship between ψ and the correlation between model parameters**

495 Our simulation showed that models with different values of parameter describing the
496 interaction between the environment and the foraging characteristics of the species (ψ) and
497 variability in both the parameter of catabolism (k_i) and the parameter describing the
498 environmental contribution to anabolism (γ_i) are in general able to describe very similar growth
499 trajectories. A clear pattern of probability of convergence of the model fitting procedure did not
500 emerge from our simulations, but model fitting was successful in the vast majority of cases. This
501 flexibility has to be ascribed to the many degrees of freedom of our formulation of the von
502 Bertalanffy growth function with individual random effects. Furthermore, when simulating
503 growth trajectories with negative or positive correlation between pairs of k_i and γ_i , the sign of
504 the correlation tended to remain negative and positive, respectively, when fitting models with
505 other values of ψ . This pattern emerged only in the case of simulated data, since a clear change
506 of sign of the correlation between pairs of k_i and γ_i was found when fitting the growth models
507 to empirical data, as described below. This has to be ascribed to some unrealistic growth
508 trajectories that are obtained when keeping the same variance for individual random effects for
509 each value of ψ used to generate the growth trajectories (Fig. A5).

510 **4.2 Case study**

511 ***4.2.1 Model selection, parameter estimates, and trade-off between accuracy and*** 512 ***interpretability in growth models***

513 All models predicted the observed data very well, although there were small differences in
514 performance among models for either population. However, when predicting growth trajectories

515 using the estimated model parameters for models with different values of ψ , for either
516 population the best model among those with no predictor for either model parameter was the one
517 predicting the highest number of crossing growth trajectories. The mean absolute error was very
518 low in each model, thus “realized” growth trajectories were almost perfectly predicted by each
519 model. It follows that the differences in predicted growth trajectories should be mostly ascribed
520 to differences in prediction of growth trajectories for fish that have been sampled one or a few
521 times early in life, i.e. the best model predicted that size ranks for the growth trajectories that
522 were not “realized” due to early mortality were less maintained (i.e. more trajectories crossing)
523 with respect to the other models.

524 Accuracy describes the ability of a model to explain observed data and make correct
525 predictions, while interpretability concerns to what degree the model allows for understanding
526 processes. Often a trade-off exists between accuracy and interpretability; more complex models
527 are usually opaque, while more interpretable models often do not provide the same accuracy or
528 predictive power of more complex models (Breiman 2001). McCullagh & Nelder (1989) wrote:
529 “Data will often point with almost equal emphasis on several possible models, and it is important
530 that the statistician recognize and accept this.” (quoted in Breiman (2001)). However, different
531 models may give different insights on the relation between the predictors (model parameters and
532 their predictors) and response variables (length-at-age), and how to determine which model most
533 accurately reflects the data remains a challenge. One way is to use model selection procedures
534 that trade off goodness-of-fit (the likelihood) and model complexity (number of parameters) to
535 select for the best model (Burnham and Anderson 2002, Johnson and Omland 2004). In our
536 work, the AIC analysis showed for either population that models with individual random effects
537 for both parameters performed substantially better than models with individual random effects
538 only for k_i . Thus, increasing the complexity of the model by allowing individual variation in
539 both parameters increased the accuracy of the growth models.

540 The best model for the marble trout population of Zakojska included cohort as a categorical
541 predictor for both γ and k , while for the brown trout population of Upper Idrijca the best model
542 included cohort as predictor of k . That means that parameter values as well as the resulting
543 predicted growth trajectories of fish seem to be more similar to those of fish in the same cohort
544 than to those of the population as a whole.

545 The prediction of mean cohort-specific growth trajectories using models with or without
546 random effects showed different results for the populations of Upper Volaja and Zakojska. For
547 the brown trout population of Upper Volaja, cohort-specific models with no random effects (i.e.
548 estimated using the *nls* function in R) and random-effects models with cohort as predictor of
549 both k_i and γ_i with either $\psi = 1$ or that of the best model provided essentially the same
550 prediction of mean cohort-specific growth trajectories. On the other hand, for the marble trout
551 population of Zakojska the random-effects models provided essentially the same predictions of
552 mean cohort-specific growth trajectories, while the cohort-specific models with no random
553 effects tended to predict substantially higher length-at-age for fish older than 4 years old. This
554 occurred because there was higher variation in length-at-age in Zakojska than in Upper Volaja
555 and some big fish tended to have a longer lifespan in Zakojska, thus growth trajectories tended to
556 be “pulled up” by the big, older individuals. This result supports the use growth models with
557 individual random effects, in particular when there is substantial variability in both growth rates
558 and size-at-age of individuals living in the same population. However, in both populations the
559 random-effects models provided essentially the same predictions of mean cohort-specific growth
560 trajectories.

561 **4.2.2 Biological interpretation of the selected growth models and parameter estimates**

562 Across taxa, climatic vagaries during the first stages of life have the potential to influence
563 the mean growth trajectories of cohorts, as well as other life histories. Empirical evidence of
564 early induced effects on later growth rate, life-history traits and behavior of organisms is quite
565 recent (Danchin and Wagner 2010, Salvanes et al. 2013, Ait Youcef et al. 2015). Jonsson and
566 Jonsson (2014) recently discussed how conditions fish encounter early in their life cycle could
567 leave lasting effects on morphology, growth rate, life-history and behavioral traits. Vincenzi et
568 al. (2014a,b) found that other processes may be potentially responsible for variability of mean
569 growth trajectories of cohorts, such as high variance in reproductive success combined with
570 either high heritability of growth or heterogeneity in site profitability accompanied by limited
571 movement. High heritability of growth (Carlson and Seamons 2008), maternal decisions on the
572 timing and location of spawning (Letcher et al. 2011), dominance established early in life
573 (Gilmour et al. 2005) are all processes that may in combination or by themselves explain the
574 maintenance of size ranks throughout fish lifetime.

575 Trade-offs between growth and survival have been found across species and taxa (Pauly
576 1980) as well as at the individual level within populations at the early life-stages (Biro and Post
577 2008, Woodson et al. 2013). Given the similarity in growth of fish in the same cohort, we may
578 hypothesize cohort effects also in survival, either in the direction of higher mortality for faster-
579 growing cohorts due to trade-offs between growth and survival, or of higher survival for faster-
580 growing cohorts when faster growth is a signal of higher quality of individuals.

581 The biological interpretation of model parameters is easier when only the individual random
582 effects (and not cohort) are included as predictors. In this case, for both populations the model
583 with $\psi = 0$ performed substantially better than the model with $\psi = 1$. This result, along with
584 the strong negative empirical correlation between estimates of k_i and γ_i when $\psi = 0$, suggests
585 that size ranks are largely maintained throughout marble and brown trout lifetime, crossing of
586 growth trajectories mostly occurs after sexual maturity, and that more aggressive/active fish are
587 on average growing slower than those less aggressive/active.

588 One hypothesis is that both trout populations live in an environment in which resource
589 acquisition depends less on intrinsic behavioral traits and more on habitat, and thus more active
590 individuals are expending more energy than less active individuals without acquiring more
591 resources. Support for this hypothesis comes from the mean bigger size-at-age found in both
592 Upper Volaja and Zakojska for trout living in the uppermost part of the streams, as more food –
593 in particular invertebrate drift - is available there.

594 As for growth trajectories crossing mostly after sexual maturity, one potential explanation is
595 sex-specific energetic investment in reproduction, with females allocating more energy to
596 reproduction than growth with respect to males.

597 **4.2.3 Predicting unobserved data**

598 The variation in growth and size that characterizes organisms can almost always be modeled
599 retrospectively. However, the limited number of attempts at predicting missing size observations
600 or unobserved growth trajectories may also depend on the intrinsic unpredictability of some
601 growth curves, for which it may be impossible to accurately predict later portions of the growth
602 trajectory when only a few observations early in life are available (e.g. ocean growth of
603 anadromous salmonids when only a few observations relative to the freshwater phase are

604 available) (Norton et al. 1976). The vBGF models with cohort as predictor of both k_i and γ_i ,
605 and $\psi = 0, 1$, or ψ of the best overall model (ψ_b) provided good predictions of unobserved
606 growth trajectories for both the marble and brown trout populations, and except for one case (
607 $\psi = \psi_b$ for Zakojska) the predictions were consistently better than predictions of the best model
608 with individual variability only for k_i and of predictions based on the mean length-at-age of the
609 fish cohort. However, neither for the marble trout population of Zakojska nor for the brown
610 population of Upper Idrijca, the best model selected according to AIC provided the best
611 prediction of unobserved growth trajectories. Although the best model did not formally overfit,
612 the additional flexibility provided by a value of ψ not equal to 0 or 1 did not translate in more
613 accurate predictions of unobserved growth trajectories.

614 **4.3 Conclusions and implications for management**

615 The purpose of a scientific investigation should drive model formulation and the type and
616 amount of data collected. Random-effects models and powerful software and routines allow the
617 fitting of complex models, but often complexity comes at the cost of interpretability of model
618 parameters. Our work shows that adding additional complexity to the von Bertalanffy growth
619 function (e.g. cohort as predictor of vBGF's parameters, variability in both k_i and γ_i) may offer
620 substantial advantages in terms of understanding of the determinants of growth patterns and
621 predicting or estimating the future or unobserved size-at-age of individuals. When using the
622 model formulation that we propose in this paper and for ease of interpretation of model
623 parameters, we recommend limiting model selection to models with $\psi = 0$ (vBGF as formulated
624 by von Bertalanffy, in which asymptotic size is an explicit function of the growth coefficient) or
625 $\psi = 1$ (vBGF as commonly fitted, in which asymptotic size is independent of the growth
626 coefficient). In those two cases, model selection may give clearer insights on processes leading
627 to individual and group variation in growth while providing accurate predictions of unobserved
628 or future size-at-age data and growth trajectories. Further insights on the processes leading to
629 variation in growth would come from combining parameter estimation and model selection with
630 estimates of metabolic rates, patchiness of resources, movement of fish and costs of
631 reproduction. Further investigation on these trade-offs are needed using other growth models and
632 other species.

633 By furthering our understanding of variation in life-history processes that depend on, or
634 correlate with, growth processes, our modeling approach has relevant implications for more
635 applied contexts. For instance, our results support the hypothesis that both trout populations live
636 in an environment in which resource acquisition depends more on habitat selection than on
637 intrinsic behavioral traits (although, especially early in life, intrinsic difference in behavioral
638 traits contributes to habitat selection). The hypothesis is also supported by the consistently bigger
639 size-at-age of fish occupying the uppermost part of the Western Slovenian streams in which
640 other marble trout populations live – where a larger portion of stream drift is available since no
641 fish are present upstream - than of those fish living further downstream (Vincenzi et al. 2010,
642 2014b, 2015). Trout are typically stationary feeders that hold relatively fixed positions from
643 which they make short forays to feed; according to our model-selection results, habitat choice or
644 chance (such as being born more upstream, especially when natural barriers reduce or impair
645 upstream movement) are critical for growth and fitness of the individual. Riverscapes are highly
646 spatially heterogeneous and the effects of habitat type and quality on individual fitness may be
647 strongest and best explained at the microhabitat spatial scale (Fausch 1984). The importance of
648 habitat selection may thus suggest the use of spatially explicit models for studying the population
649 dynamics of the two species, as well as for predicting the evolution of growth and other life-
650 history traits (Ayllón et al. 2015).

651 Estimates of growth are also fundamental to any assessment of population demographics
652 and population dynamics for management. For instance, age-structured stock assessment
653 methods are based on size-at-age that is often derived from parameters of the von Bertalanffy
654 growth model for that species (Katsanevakis and Maravelias 2008). We have shown that for the
655 salmonid populations that we used as a model system, our model allows one to use a single
656 measurement early in the life of individual fish (or, equivalently, a set of measurements from a
657 cohort) to obtain accurate predictions of lifetime individual or cohort size-at-age.

658

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660

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668

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859 Ecological Archives

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861 **Figure A1.** Growth trajectories with $\sigma_u = \sigma_v = 0.14$, $L_\infty = 300$ mm (mean across all
862 individuals), $t_0 = -0.32$ mm, $k_0 = 0.38$ y⁻¹ (mean across all individuals).

863 **Figure A2.** Growth trajectories with $\sigma_u = \sigma_v = 0.6$, $L_\infty = 300$ mm (mean across all
864 individuals), $t_0 = -0.32$ mm, $k_0 = 0.38$ y⁻¹ (mean across all individuals).

865 **Figure A3.** Results of reciprocal fitting with $L_\infty = 300$ mm, $t_0 = -0.32$ mm, $k_0 = 0.38$ y⁻¹,
866 $\sigma_u = \sigma_v = 0.14$, $\gamma_0 = L_\infty(k_0^{1-\varphi})$, $M = 0.8$, and correlation r_s between k_i and γ_i equal to -0.9.

867 **Figure A4.** Results of reciprocal fitting with $L_\infty = 300$ mm, $t_0 = -0.32$ mm, $k_0 = 0.38$ y⁻¹,
868 $\sigma_u = \sigma_v = 0.60$, $\gamma_0 = L_\infty(k_0^{1-\varphi})$, $M = 0.8$, and correlation r_s between k_i and γ_i equal to -0.9.

869 **Figure A5.** Examples of growth trajectories simulated with $\psi_s = 1$, $L_\infty = 300$ mm,
870 $t_0 = -0.32$ mm, $k_0 = 0.38$ y⁻¹, $\sigma_u = \sigma_v = 0.60$, $\gamma_0 = L_\infty(k_0^{1-\varphi})$, $M = 0.8$, and correlations r_s
871 between k_i and γ_i equal to -0.9, 0, 0.9.

872 **Text A1.** Description of trade-offs between data requirements, model accuracy, and
873 biological interpretability of parameters in the Dynamic Energy Budget (DEB) growth model
874 and in the logistic growth model.

875

876 Tables

877

878 **Table 1.** Model parameters, model assumptions, and data-generating parameter values or
 879 their empirical estimates/relationship.

880

Parameter	Description
L_{∞}	Asymptotic length reached in the limit of infinite time
k	Coefficient of catabolism or vB growth coefficient
t_0	Age at which length is 0
q	Coefficient of anabolism
γ	Parameter describing the environmental contribution to anabolism
ψ	Parameter bounded between 0 and 1 describing the interaction between the environment and the foraging characteristics of the species
k_0 and γ_0	Population-level parameters in the linear models for $\log(k)$ and $\log(\gamma)$
α and β	Group-level parameters in the linear models for $\log(k)$ and $\log(\gamma)$
u and v	Standardized individual random effects in the linear models for $\log(k)$ and $\log(\gamma)$
σ_u and σ_v	Standard deviations of the statistical distributions of the random effects in the linear models for $\log(k)$ and $\log(\gamma)$
Model assumptions	
$L_{\infty} = \frac{q}{k}$	Asymptotic size emerges from the relationship between the coefficients of anabolism and catabolism
$q = \gamma k^{\psi}$	The coefficient of anabolism q depends on environmental (represented by γ) versus behavioral (represented by k) factors, whose respective importance is modulated by the value of the parameter ψ
Estimated/data-generating parameter values and relationship between parameter values	
ψ_s	Data-generating ψ
r_s	Data-generating Pearson's correlation between individual-level pairs of k and γ
ψ_f	Fixed value of ψ when fitting length-at-age data
r_f	Empirical correlation between estimated pairs of k and γ

881

882 **Table 2.** The ten best von Bertalanffy growth models according to AIC for the marble trout
 883 population of Zakojska and the brown trout population of Upper Volaja. Parameters included in
 884 the model column are those that are a function of cohort. *npar* is the number of model
 885 parameters; AIC = Akaike Information Criterion. The last row reports the best models when
 886 individual random effects are included only for *k*.

887

Zakojska				Upper Volaja			
Model	ψ	AIC	npar	Model	ψ	AIC	npar
k, γ	0.3	17 105	29	γ	0.6	23 269	19
k, γ	0.4	17 106	29	k, γ	0.5	23 277	31
k, γ	0.2	17 112	29	k, γ	0.6	23 283	31
k, γ	0.1	17 123	29	γ	0.5	23 303	19
k, γ	0.5	17 127	29	k, γ	0.3	23 328	31
k, γ	0	17 132	29	k, γ	0.2	23 338	31
γ	0.4	17 137	20	k, γ	0.4	23 346	31
γ	0.3	17 144	20	γ	0.4	23 348	19
k, γ	0.6	17 153	29	k, γ	0	23 350	31
γ	0.2	17 159	20	k, γ	0.7	23 363	31
k, γ	0.4	17 831	27	k, γ	0.6	24 977	27

888

889 **Table 3.** Mean \pm sd of R^2 and mean absolute error (MAE, mm) of predictions of validation data for 10 random validation samples
 890 as provided by (a) the vBGF model with variation for both for both k and γ (vBGF (k_i, γ_i)) including cohort as predictor for both k and
 891 γ with $\psi = 0, 1$, and ψ of the best model according to AIC ($\psi = 0.5$ for Upper Volaja and $= 0.3$ for Zakojska), (b) the vBGF model
 892 with variation for only k (vBGF (k_i)) including cohort as predictor for both k and γ with ψ of the best model according to AIC ($\psi =$
 893 0.6 for Upper Volaja and $= 0.4$ for Zakojska). We also report mean \pm sd of R^2 and MAE of predictions with mean length-at-age of the
 894 respective cohorts (Cohort).

895

	vBGF (k_i, γ_i)						vBGF (k_i)		Cohort	
Population	$\psi = 1$		$\psi = 0$		best ψ		best ψ			
	R^2	MAE	R^2	MAE	R^2	MAE	R^2	MAE	R^2	MAE
Zakojska	0.61 \pm 0.22	32.0 \pm 13.0	0.54 \pm 0.22	35.1 \pm 12.3	0.52 \pm 0.16	36.3 \pm 9.5	0.44 \pm 0.07	38.2 \pm 5.46	0.52 \pm 0.09	36 \pm 5.1
U Volaja	0.57 \pm 0.21	15 \pm 3.4	0.56 \pm 0.2	15.2 \pm 3.3	0.55 \pm 0.21	15.2 \pm 4.2	0.47 \pm 0.09	17.2 \pm 1.23	0.51 \pm 0.2	16 \pm 2.9

896 **Figure captions**

897

898 **Figure 1.**

899 **Panel (a)** Mean age at growth trajectories crossing, number of trajectories crossing divided
900 by the total number of individuals (Norm traj crossing), and coefficient of variation of length at
901 age 10 (CV of length) for von Bertalanffy growth models as in Eqs. 2.7 and 2.8 with different
902 values of ψ and Pearson's correlation between pairs of k_i and γ_i . Panels in the same column
903 are for models with the same correlation between pairs of k_i and γ_i . For all models, individuals
904 have the same asymptotic length $L_\infty = 300$ mm, $t_0 = -0.32$ y, $k_0 = 0.38$ y⁻¹, $\sigma_u = \sigma_v = 0.36$,
905 $\gamma_0 = L_\infty(k_0^{1-\varphi})$. Vertical segments are standard deviations over 10 replicates with random drawing
906 of individual random effects to simulate individual growth trajectories.

907 **Panel (b)** Ten growth trajectories simulated with the model in Eq. 2.8 and the same
908 parameter estimates as in panel (a). From left to right column, correlation between k_i and γ_i
909 equal to -1, 1, ~0. From top to bottom row, ψ equal to 0, 0.5, 1.

910 **Figure 2.** Frequency of sampling events per individual and empirical growth trajectories for
911 the populations of Upper Volaja (brown trout) and Zakojska (marble trout).

912 **Figure 3.** Panels (a-c): average Pearson's correlation \bar{r}_f between k_i and γ_i across
913 replicates that successfully converged when fitting von Bertalanffy growth models as in Eqs. 2.7
914 and 2.8 with $\psi = \psi_f$ on growth trajectories simulated with $\psi = \psi_s$, $L_\infty = 300$ mm, $t_0 = -0.32$ y,
915 $k_0 = 0.38$ y⁻¹, $\sigma_u = \sigma_v = 0.37$, $\gamma_0 = L_\infty(k_0^{1-\varphi})$, mortality rate $M = 0.8$, and correlation r_s between
916 k_i and γ_i equal to -0.9 (panels a,d), 0 (b,e), 0.9 (c,f). Panels (d-f): Number of replicates F that
917 did not converge for every combination of ψ_s and ψ_f out of the 10 replicates. Plots for
918 $\sigma_u = \sigma_v = 0.60$ and $\sigma_u = \sigma_v = 0.14$ are provided in Supplementary Material (Figures A3 and
919 A4).

920 **Figure 4.** Correlation (Pearson's r) between estimates of k_i and γ_i for different values of
921 ψ for the von Bertalanffy growth model with no predictors other than individual random effects
922 for either k and γ for Zakojska (gray) and Upper Volaja (black). Vertical segments are 95%
923 confidence intervals of r . The best model with no predictors other than individual random effects
924 according to AIC for Upper Volaja and Zakojska had $\psi = 0.6$ and $\psi = 0.4$, respectively.

925 **Figure 5.** Mean age at crossing of growth trajectories, total number of trajectories crossing
926 divided by the total number of individuals in the population (1649 for Upper Volaja and 1147 for
927 Zakojska), and coefficient of variation of length at age 10 for von Bertalanffy growth models
928 (with no predictors except individual random effects for either model parameter) with model
929 parameters estimated for values of ψ from 0 to 1 with step 0.1. All growth trajectories of
930 unique individuals were predicted for a theoretical lifespan of 10 years according to the
931 estimated model parameters at the individual level. Vertical lines identify the best model
932 according to AIC for models with no predictors for either parameter.

933 **Figure 6.** Cohort-specific growth trajectories for the trout populations of Zakojska (panel a,
934 Cohort 1999; b, C01) and Upper Volaja (panel c, C08; d, CO7). Dashed line: prediction of model
935 with no random effects fitted on cohort data with non-linear least square regression. Dash-dot
936 line: Cohort-specific model with cohort as predictor for both k_i and γ_i with $\psi = 0.3$ and $\psi = 0.5$
937 (best models) for Zakojska and Upper Volaja, respectively. Solid line: Cohort-specific model
938 with cohort as predictor for both k_i and γ_i with $\psi = 1$.

939 **Figure 7.** Example of prediction of validation data for the marble trout population of
940 Zakojska with the von Bertalanffy growth model with cohort as predictor of k_i and γ_i and $\psi = 1$
941 (panel a), $\psi = 0.3$ (b, best model), $\psi = 0$ (c). Panel (d) reports the prediction of validation data
942 using mean length-at-age for the cohort of the individual whose growth is predicted.

943 **Figure 8.** Example of prediction of validation data for the brown trout population of Upper
944 Volaja with the von Bertalanffy growth model with cohort as predictor of k_i and γ_i and $\psi = 1$
945 (panel a), $\psi = 0.3$ (b, best model), $\psi = 0$ (c). Panel (d) reports the prediction of validation data
946 using mean length-at-age for the cohort of the individual whose growth is predicted.

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Figure 1

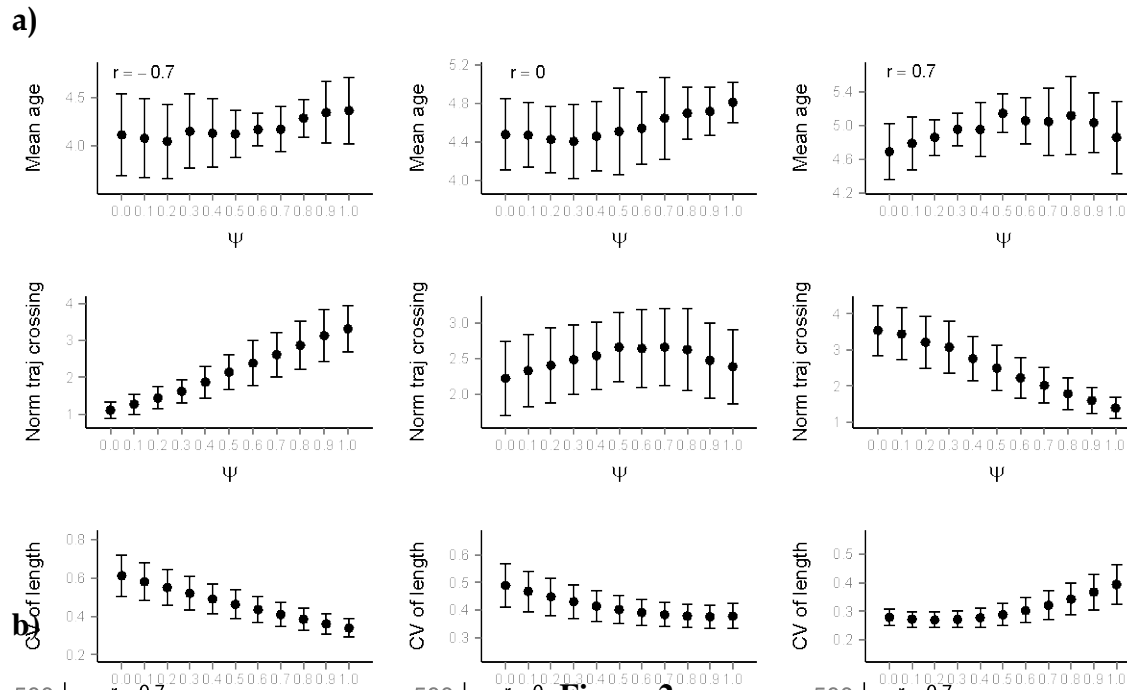
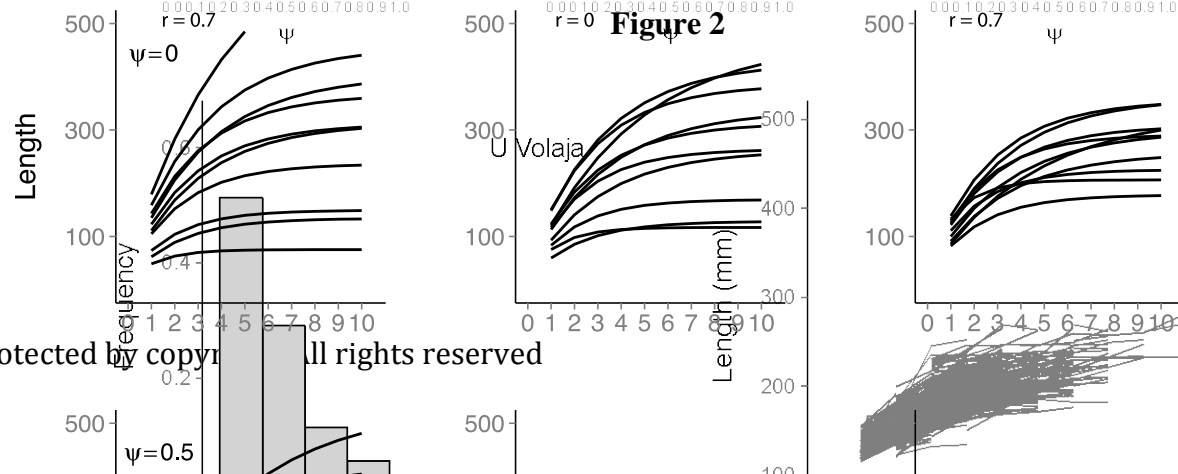


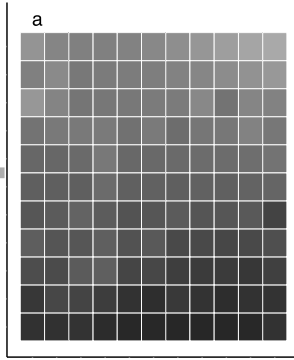
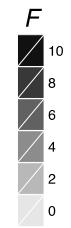
Figure 2

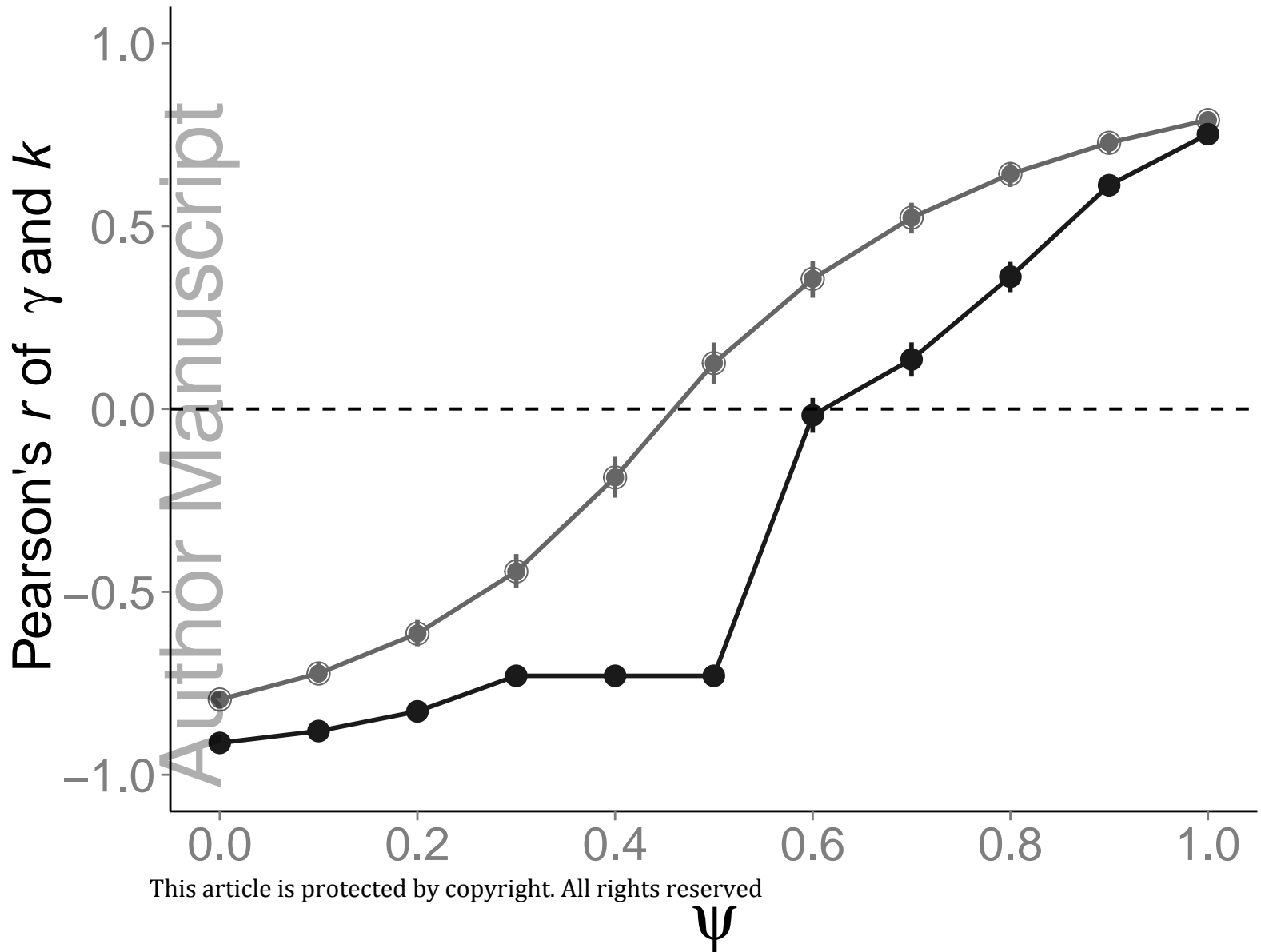


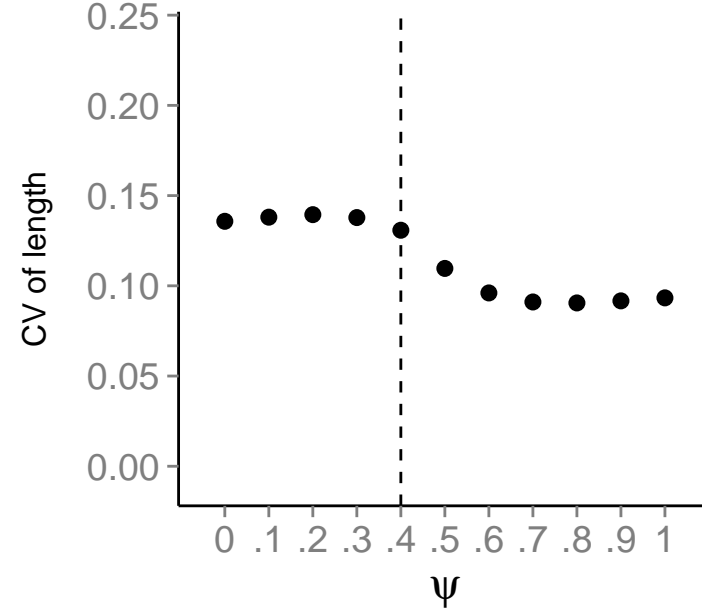
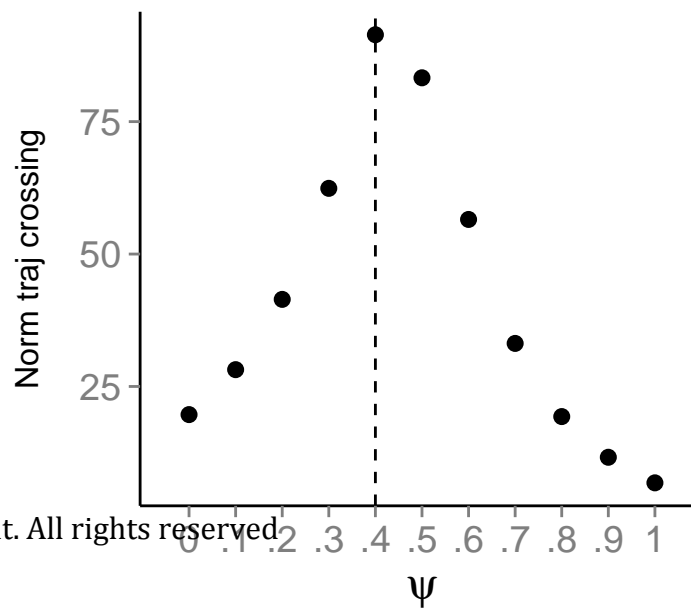
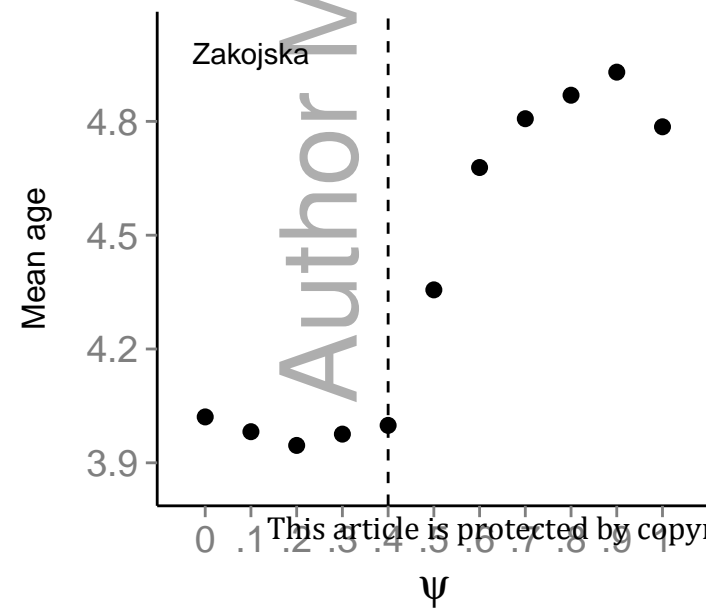
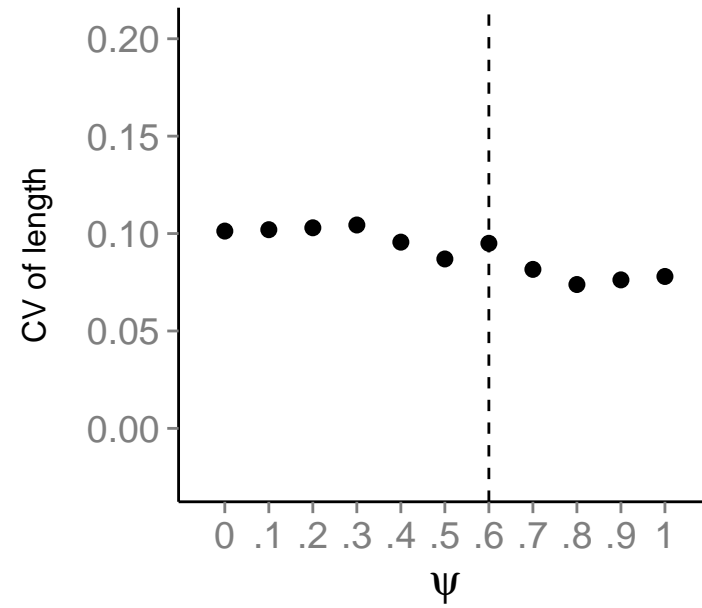
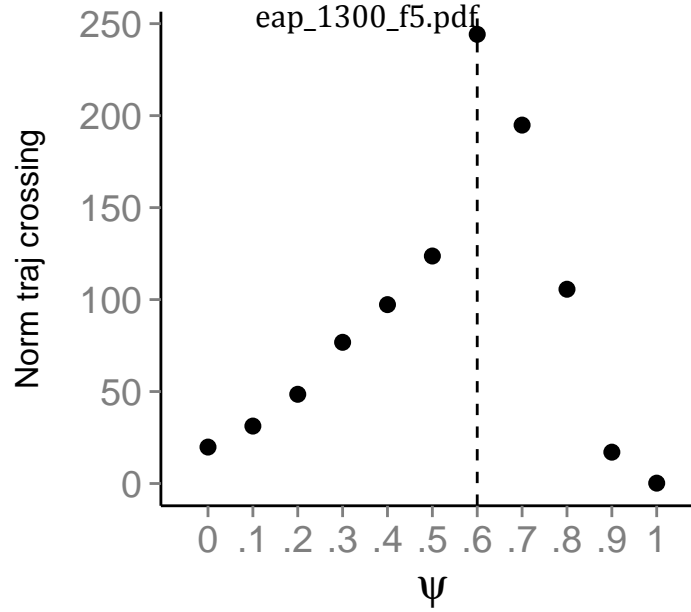
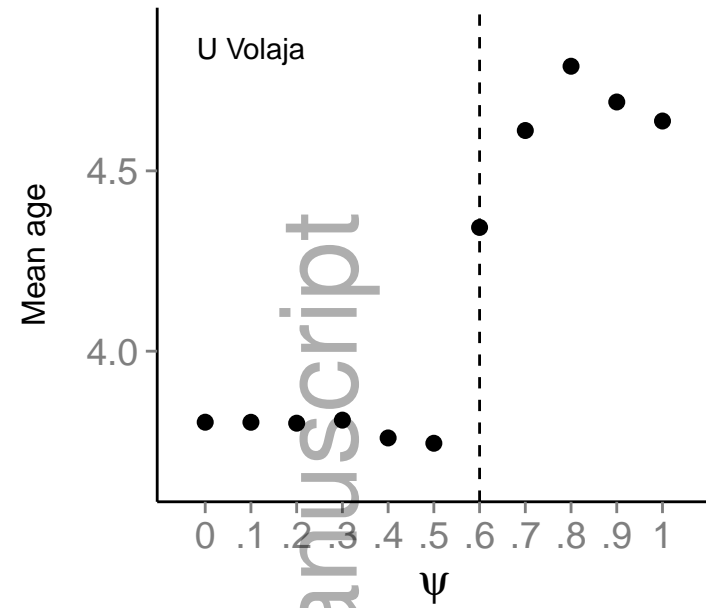
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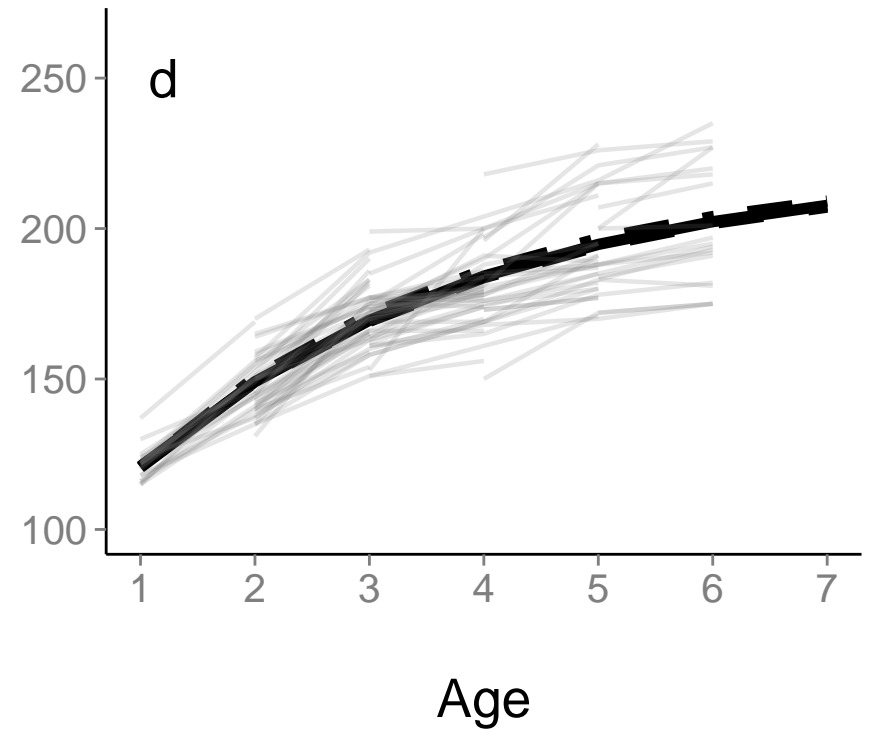
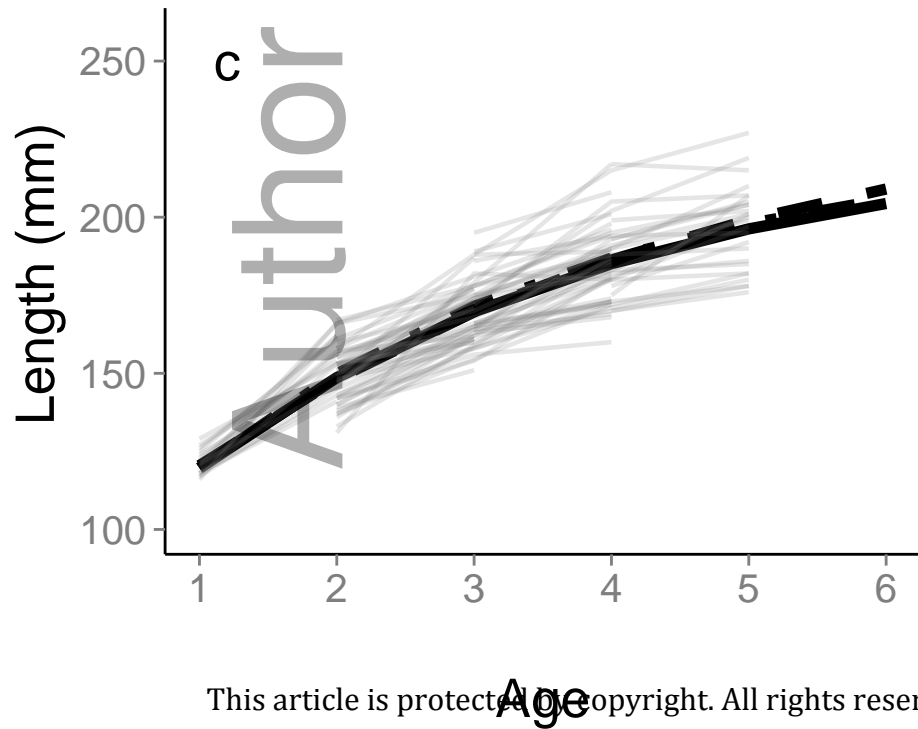
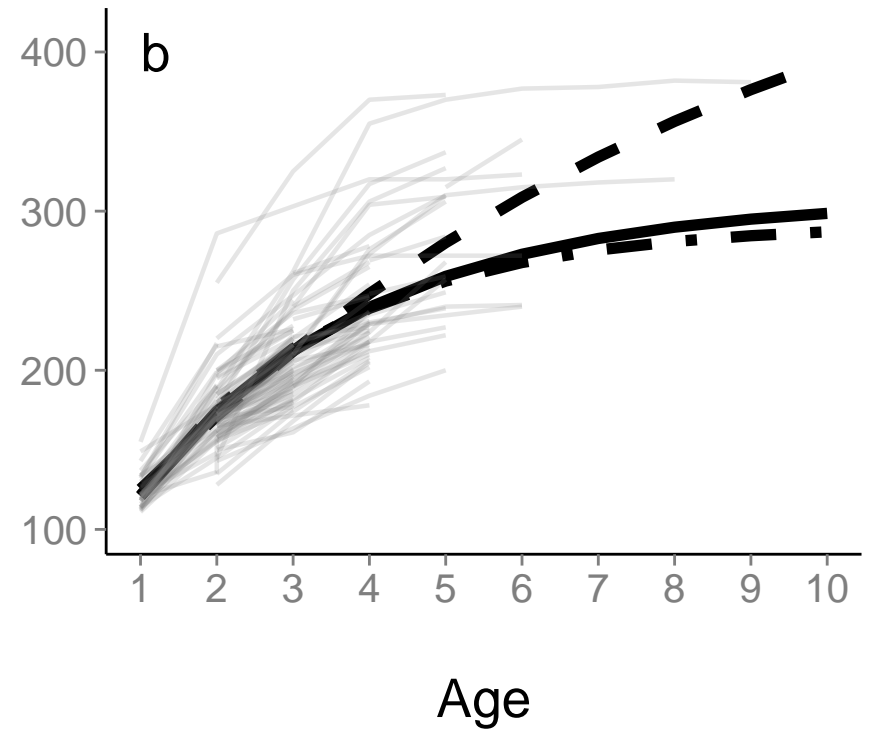
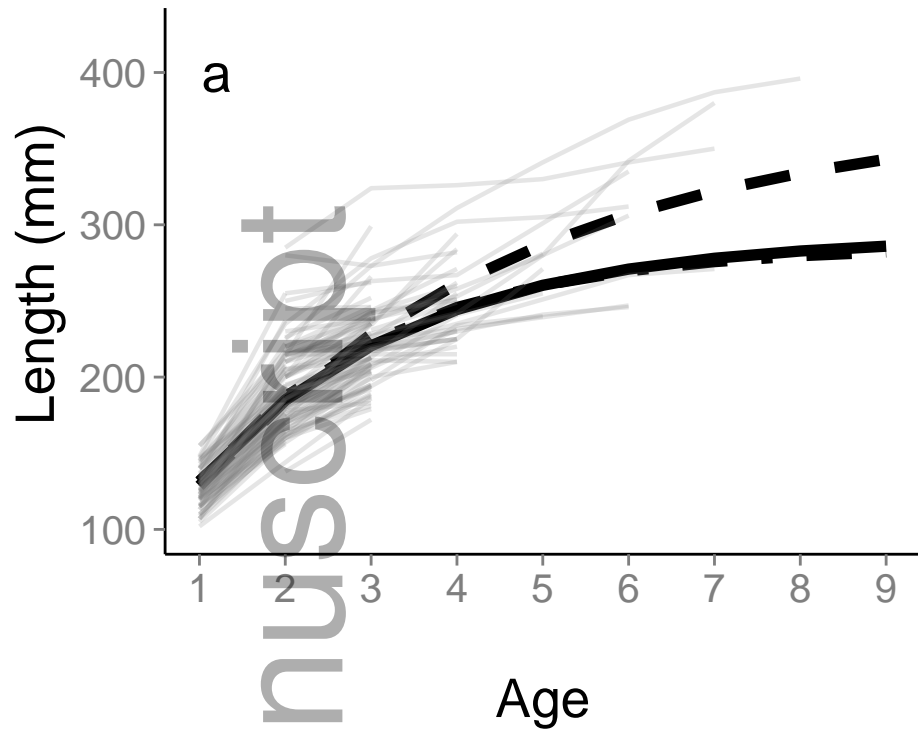
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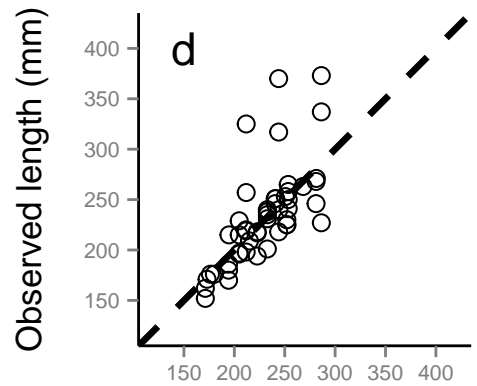
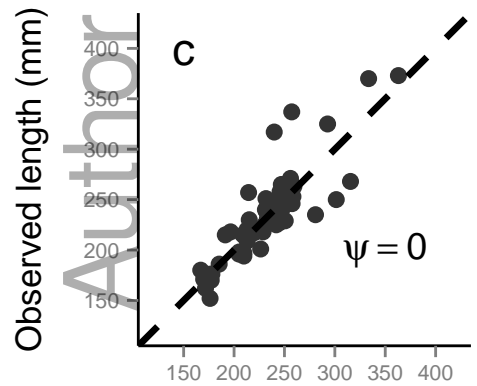
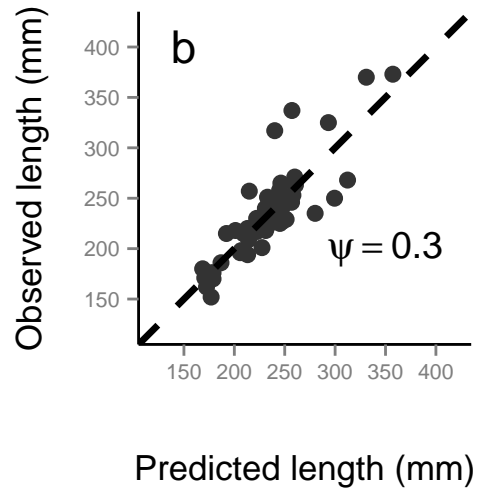
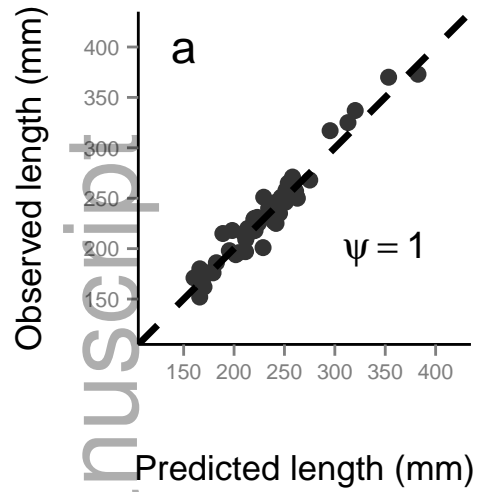
Figure 3

 Ψ_f Ψ_s 









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Predicted length (mm)

Predicted length (mm)

