1 **The energetics of fish growth and how it constrains food-web trophic structure**

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ABSTRACT

The allocation of metabolic energy to growth fundamentally influences all levels of biological organization. Here we use a first-principles theoretical model to characterize the energetics of fish growth at distinct ontogenetic stages and in distinct thermal regimes. Empirically, we show that the mass scaling of growth rates follows that of metabolic rate, and is somewhat steeper at earlier ontogenetic stages. We also demonstrate that the cost of growth, E_m, varies substantially among fishes, and that it may increase with temperature, trophic level, and level of activity. Theoretically, we show that E_m is a primary determinant of the efficiency of energy transfer across trophic levels, and that energy is transferred more efficiently between trophic levels if the prey are young and sedentary. Overall, our study demonstrates the importance of characterizing the energetics of individual growth in order to understand constraints on the structure of food webs and ecosystems.

INTRODUCTION

Organisms must expend energy to gather, consume, and transform the resources necessary to produce biomass, so the rate of biomass production is fundamental at multiple biological levels (Lindeman 1942). At the individual level, it influences fitness by constraining how quickly an organism reaches maturity and subsequently produces offspring (Brown *et al.* 1993). At the population level, it constrains the intrinsic rate of population increase (Savage *et al.* 2004). At the community level, it constrains how much energy and materials can flow to the next trophic level in a food web (Andersen *et al.* 2009; Irigoien *et al.* 2013). And, at the ecosystem level, the fraction of assimilated energy lost in producing that biomass (through respiration) limits the total heterotrophic metabolism, and hence the number of trophic levels, that can be supported in a food web (Lindeman 1942; Pauly & Christensen 1995).

We still lack a comprehensive theoretical understanding of the energetics of growth, despite recent progress (e.g. West *et al.* 2001; Hou *et al.* 2008; Kooijman 2009). Fish are excellent model organisms for evaluating such a theory because they encompass the highest global species richness among vertebrates (> 33,000 species), they range in body mass by over > 8 orders of magnitude (~0.1 g – 1×10^7 g), and they occupy diverse freshwater and marine habitats that vary substantially in thermal regime (~0 – 40°C; Froese & Pauly 2017).

52 Understanding the energetics of growth is of immense practical importance. For example, in

53 fisheries management, knowing how long wild fish stocks take to achieve maturity, and how

54 much food they need to do so, is crucial for establishing sustainable yields in fisheries man-

55 agement (Szuwalski *et al.* 2017). Moreover, sustainable yields at ocean-basin scales may in

56 the future be affected by changes in environmental variables such as temperature through their

57 effects on the growth energetics of individual fish (e.g. van Rijn *et al.* 2017). Extensive em-

58 pirical work has documented determinants of fish growth (e.g. Houde 1989); however, these

59 studies have typically focused on how one or few species at a particular life stage respond to

60 a particular set of environmental conditions. With few notable exceptions (see, for example,

61 Pauly & Pullin 1988; Houde 1989; Charnov & Gillooly 2004; Sibly *et al.* 2015), there has

62 been little attempt to generalize determinants of individual-level biomass production across

63 multiple fish species within a theoretical framework.

64   Theoretical work on the mechanisms underlying growth dynamics has focused primarily

65 on understanding why individuals tend to follow a sigmoid growth trajectory over ontogeny

66 such that mass-specific growth rate is rapid during early life stages, but slows down as indi-

67 viduals approach an asymptotic adult size. More than half a century ago, Ludwig von Berta-

68 lanffy (1938) proposed that these sigmoid growth trajectories arise because the overall rate

69 of catabolism increases more rapidly with size than the rate of anabolism. While the mecha-

70 nistic basis of this model (hereafter BGM) has been questioned by many, including fisheries

71 scientists (e.g. Enberg *et al.* 2008), the BGM is frequently employed for fish because it of-

72 ten provides a reasonable statistical fit to ontogenetic growth data. Importantly, however, the

73 BGM is usually fitted using widely-available data on fish length, rather than less-available

74 data on mass, which is unfortunate given that growth is fundamentally an energetic process,

75 and that the energetic costs of growth are related to changes in mass (West *et al.* 2001; Hou *et*

76 *al.* 2008; Moses *et al.* 2008).

77   West *et al.* (2001) proposed an ontogenetic growth model (see also Gillooly *et al.* 2002;

78 Moses *et al.* 2008) that is based on principles of allometry and mass and energy balance. Hou

79 *et al.* (2008) subsequently expanded this model (hereafter OGM) by explicitly partitioning

80 the total metabolic rate into active, growth, and maintenance components. Consequently,

81 the OGM predicts that growth rates are inextricably linked to the size- and temperature-

82　dependencies of metabolic rate, consistent with empirical data (Pauly & Pullin 1988; Houde

83　1989; Atkinson 1994; Gillooly *et al.* 2002; Brown *et al.* 2004). Although the OGM can be

84　mathematically similar in functional form to the BGM (Makarieva *et al.* 2004), its conceptual

85　foundations are fundamentally different. In particular, while growth is an anabolic process,

86　maintenance in the OGM involves both anabolism and catabolism because, for example,

87　protein turnover is fueled by respiration.

88　　　Of particular relevance, the OGM reveals the importance of a particular parameter, E_m,

89　which is the amount of energy that must be expended in respiration to produce a fixed quan-

90　tity of biomass (West *et al.* 2001; Hou *et al.* 2008; Moses *et al.* 2008). This quantity has

91　been shown to vary substantially within and among different clades of animals (Wieser 1994;

92　Moses *et al.* 2008; Sears *et al.* 2012). However, to our knowledge, is still unknown to what

93　extent this variation reflects differences in physiology versus environmental and/or ecological

94　factors. Understanding how and why E_m varies is fundamental because, as we will demon-

95　strate later, this quantity constrains food-web structure via its effects on the efficiency of en-

96　ergy transfer between trophic levels.

97　　　In this study, we use the OGM as a framework to characterize the mass and temperature

98　dependence of growth rates for marine and freshwater fishes. In so doing, we first quantify

99　the fraction of total metabolic energy allocated to biomass production across different species

100　at differing life stages and temperature regimes. Using these data, we then test three hypothe-

101　ses: *H1: Growth rates exhibit the same mass scaling exponent as metabolic rate at different*

102　*ontogenetic stages*; *H2: E_m is temperature independent*; and *H3: E_m is independent of eco-*

103　*logical variables such as trophic level and level of activity*. Finally, we combine our empirical

104　estimates of E_m with novel theory to explore how it constrains food-web structure through its

105　effects on the efficiency of energy transfer between trophic levels.

106　**MATERIALS AND METHODS**

107　*1. Theory and hypotheses*

108　*Hypothesis H1*

109　The OGM (West *et al.* 2001; Hou *et al.* 2008) is derived based on energy balance for an or-

110   ganism with a wet mass of m (in g), a resting metabolic rate of B_r (i.e. J d^{-1}), and a growth rate

111   per unit time, t (d), of dm/dt (g d^{-1}),

$$\frac{dm}{dt} = \frac{B_r}{E_m}\left[1 - \left(\frac{m}{M}\right)^{1-\alpha}\right] = \frac{B_o(T)}{E_m}m^\alpha\left[1 - \left(\frac{m}{M}\right)^{1-\alpha}\right], \quad (1)$$

112   where $B_r = B_o(T)m^\alpha$, $B_o(T)$ is a metabolic normalization constant independent of body mass

113   (J $g^{-\alpha}$ d^{-1}) that varies among fish taxa and with absolute body temperature (Barneche *et al.*

114   2014), T(K), α is a dimensionless mass-scaling exponent that is theoretically predicted to take

115   a value of 3/4 in the fractal-like distribution model of West *et al.* (1997), and E_m is the en-

116   ergy expended to produce one unit of biomass (J g^{-1}). The expression $[1 - (m/M)^{1-\alpha}]$ is the

117   fraction of resting metabolic energy that is allocated to growth. This fraction approaches 0 as

118   the organism approaches its asymptotic adult mass, M, at which point all resting metabolic

119   energy is allocated to maintenance, which is assumed to remain constant on a mass-specific

120   basis over ontogeny.

121   *Hypothesis H1: Growth rates exhibit the same mass scaling exponent as metabolic rate at*

122   *different ontogenetic stages*. The OGM states that the mass scaling of growth rates are gov-

123   erned by the effects of body mass on resting metabolic rates, B_r. Empirically, it has been ob-

124   served that early in ontogeny, the scaling of metabolic rates in fish can be substantially steeper

125   (Bochdansky & Leggett 2001) than the canonical 3/4 value observed for adult fish (Barneche

126   *et al.* 2014). Whether these shifts in metabolic mass scaling over ontogeny are also observed

127   for growth rates remains poorly explored. However, this phenomenon can be empirically

128   assessed by fitting growth-rate data at different ontogenetic stages to a function of the same

129   form as that commonly fitted to metabolic rates (eqns S1–S3),

$$\frac{dm}{dt} = g_o m^\gamma e^{\frac{E_g}{k}\left(\frac{1}{T_s} - \frac{1}{T}\right)} I(T)^{-1}, \quad (2)$$

130   where g_o is a normalized growth rate that is independent of mass and temperature (g

131    $^{1-\gamma}$ d^{-1}) at some arbitrary standardized temperature, T_s (K), k is the Boltzmann con-

132   stant (8.62×10^{-5} eV K^{-1}), γ is a dimensionless mass-scaling exponent, and E_g (eV)

133   is an activation energy (Barneche *et al.* 2014). With respect to size, eqn 1 predicts that

134 $g_o \propto [1 - (m/M)^{1-\alpha}]$, implying a decline in normalized rates with increasing ontogenetic

135 stage, m/M. With respect to temperature, $e^{\frac{E_g}{k}\left(\frac{1}{T_s} - \frac{1}{T}\right)}$ is the Boltzmann relationship that char-

136 acterizes temperature-induced enhancement of growth rates below the temperature optimum,

137 T_{opt} (K), using an activation energy, E_g (eV) (Gillooly *et al.* 2002). The inactivation term,

138 $I(T) = \left(1 + \left(\frac{E_g}{E_i - E_g}\right) e^{\frac{E_i}{k}\left(\frac{1}{T_{opt}} - \frac{1}{T}\right)}\right)$, characterizes declines in rates at temperature T above

139 T_{opt} using an inactivation parameter, E_i (Schoolfield *et al.* 1981; Barneche *et al.* 2014).

140 *Hypotheses H2–H3*

141 The respiratory energy expended in producing a unit of biomass, E_m, can be calculated by

142 rearranging eqn 1:

$$E_m = B_r \frac{dt}{dm}[1 - (m/M)^{1-\alpha}]. \tag{3}$$

143 In practice, calculating E_m using eqn 3 requires ontogenetic growth data in order to estimate

144 $[1 - (m/M)^{1-\alpha}]$. In the absence of such data, an upper bound estimate for E_m, E_m^*, can be

145 calculated using estimates of growth rate taken early in ontogeny

$$E_m^* \approx B_r \frac{dt}{dm}, \tag{4}$$

146 when the mass of an individual is negligible compared to the asymptotic adult mass, $m << M$

147 (Moses *et al.* 2008).

148   The quantity E_m reflects energy allocated to growth via both direct and indirect paths (Hou

149 *et al.* 2008). Thus, its magnitude does not correspond to the combustion energy (i.e. chemical-

150 energy content) of assimilated biomass (Makarieva *et al.* 2004). Rather, it corresponds to

151 the sum of all direct and indirect energy costs that an individual must expend in producing

152 biomass. The direct costs of synthesizing biomass may, in fact, be lower than the combustion

153 energy because, for example, proteins may be constructed from pre-formed amino acids as-

154 similated from food. The indirect costs include other processes that are not directly related to

155 biomass production, but that are nevertheless essential for this production to occur (e.g. diges-

156 tion). While disentangling and quantifying the processes contributing to E_m are challenging,

157 the overall magnitude of E_m can nevertheless be quantified based on eqns 3 and 4.

158   *Hypothesis H2: E_m is temperature independent*. In the OGM, the temperature dependence

159   of growth rates is assumed to be governed by the effects of temperature on the resting

160   metabolic rate normalization, $B_o(T)$ (eqn 1; Gillooly *et al.* 2002). A corollary of this assump-

161   tion is that E_m is invariant with respect to environmental temperature. This hypothesis can be

162   readily assessed by investigating the relationship between empirically-estimated values of E_m

163   (eqns 3 and 4) and the environmental temperature at which organisms grow.

164   *Hypothesis H3: E_m is independent of ecological variables such as trophic level and level*

165   *of activity*. While the OGM assumes invariance of E_m over ontogeny, it currently makes no

166   predictions regarding variation in E_m among species. In fact, it is known empirically that E_m

167   varies across multiple clades of animals (Wieser 1994; Moses *et al.* 2008; Sears *et al.* 2012).

168   For fish, the possible causes for this variation are still unknown, but may be related to ecologi-

169   cal variables. For instance, fishes at higher trophic levels may have generally higher E_m values

170   at least in part because trophic level is positively associated with muscle protein (Killen *et al.*

171   2016), which may be expensive to generate. For similar reasons, caudal aspect ratio ($= h^2/s$,

172   where h is the height of the caudal fin and s its surface area), a proxy for activity level (Froese

173   & Pauly 2017), may also be positively correlated with E_m. Here we explore these ideas using

174   Hypothesis *H3*, invariance of E_m, as a null expectation.

175   *The role of E_m in constraining trophic efficiency and food-web structure*

176   Understanding how and why E_m varies is of fundamental importance to predicting constraints

177   on the efficiency of energy transfer between trophic levels (Economo *et al.* 2005; Andersen

178   *et al.* 2009). In fact, E_m is a primary determinant of the fraction of assimilated food that is

179   transferable to the next trophic level, as we will now show. The rate of energy assimilation by

180   an individual of size m, $A(m)$, is (Hou *et al.* 2008)

$$A(m) = B_{tot} + E_c \frac{dm}{dt} = fB_r + E_c \frac{B_r}{E_m}\left[1 - \left(\frac{m}{M}\right)^{1-\alpha}\right] =$$
$$B_o(T)m^\alpha\left[f + \frac{E_c}{E_m}\left[1 - \left(\frac{m}{M}\right)^{1-\alpha}\right]\right], \tag{5}$$

181   where E_c is the combustion energy of biomass (~24 kJ g^{-1} dry mass; Hou *et al.* 2008), and

182 B_{tot} is the total (i.e. field) metabolic rate, which is defined as the sum of the resting metabolic

183 rate, B_r, and the active rate that sustains locomotion, feeding, and other activities. Following

184 Hou *et al.* (2008), we assume that $B_{tot} = fB_r$ in the expression above, where f is a dimen-

185 sionless parameter referred to as 'activity scope', which is constrained to be greater than 1 and

186 less than the ratio of maximum metabolic rate to resting metabolic rate (i.e. "factorial aero-

187 bic scope" sensu Killen *et al.* 2016). Using eqns 1, 3 and 5, we can calculate the fraction of

188 energy assimilated by a prey individual, ε, that is transferred to the next trophic level through

189 consumption of prey biomass by a predator. This fraction is calculated by taking the ratio of

190 the amount of energy contained in a prey item consumed at size m, $E_c m$, and the total *lifetime-*

191 *integrated* amount of energy that the prey item has assimilated from birth to its age at con-

192 sumption, t^*,

$$\varepsilon = \frac{E_c m}{\int_{t=0}^{t^*} A\left(m(t)\right) dt}, \qquad (6)$$

193 where $m(t)$ is mass at age t (eqns S4–S6), and $t^* = -E_m \ln\left[1 - \left(\frac{m}{M}\right)^{1-\alpha}\right] / (B_o(T)M^{1-\alpha}(1-$

194 $\alpha))$ is an approximation to the age at which the prey was consumed, assuming that the prey's

195 mass at birth m_0, is negligible relative to its asymptotic size ($m_0/M \approx 0$ in eqn S6). Eqn 6

196 quantitatively predicts that if a prey individual is consumed by a predator at an earlier life his-

197 tory stage, $m/M \approx 0$, a larger fraction of the prey's assimilated energy, ε, will be transferable

198 to its predator. It is important to note that these efficiencies represent upper-bound estimates

199 because they only incorporate energy losses attributable to the respiration of the prey, and thus

200 exclude other factors affecting the energy transfer (e.g. food assimilation efficiency by preda-

201 tors). Eqn 6 can be readily integrated numerically to calculate how maximum transfer effi-

202 ciency, ε, changes with E_m, relative ontogenetic stage, m/M, and activity scope, f.

203   We can also use eqn 6 to expand theoretical predictions obtained from a static size-

204 spectrum model (Brown & Gillooly 2003). This model predicts a specific relationship

205 between total biomass, W, and individual body mass, m,

$$W \propto m^{1 + \frac{\ln(\varepsilon)}{\ln(PPMR)} - \alpha}, \qquad (7)$$

8

206 based on the size-scaling of metabolic rate (α) and the assumptions that the predator-prey

207 body-mass ratio, *PPMR*, and the efficiency of energy transfer between trophic levels, ε, are

208 held constant moving between trophic levels (Brown & Gillooly 2003).

209 *2. Data compilation*

210 We use two independent datasets to test hypotheses *H1–H3*. Dataset I comprises 179 exper-

211 imentally measured paired estimates of growth rate (g wet mass d^{-1}) and metabolic rate (J

212 d^{-1}) taken early in ontogeny (25 measurements for embryos and 154 measurements for lar-

213 vae), meaning that $m/M \approx 0$, and hence that $[1 - (m/M)^{1-\alpha}] \approx 1$. These data encompass 18

214 species of marine and freshwater fishes with body masses of $9\,\mu g - 0.5$ g and temperatures of

215 $3 - 28°C$ (Supplementary Information).

216   Dataset II was obtained from FishBase (Froese & Pauly 2017). It contains 2,849 sets of pa-

217 rameter estimates, corresponding to 2,849 ontogenetic growth curves, that were obtained by

218 fitting the von Bertalanffy growth model (BGM) (von Bertalanffy 1957) to age and size data

219 collected from 503 species of marine and freshwater fish species. As is the tradition in fish-

220 eries science, these growth curves were characterized using *length* rather than mass. To ob-

221 tain standardized mass-based estimates of growth rate, we calculate optimum (i.e. maximum)

222 growth rates, g_{opt}, at mass m_{opt}, by combining these length-based data with species-specific

223 estimates of the mass-length conversion parameters. These g_{opt} estimates encompass 62 fam-

224 ilies and a temperature range of -0.9–30°C. In the Supplementary Information, we derive an

225 analytical approximation (eqns S4–S16) that justifies using BGM-estimated optimum growth

226 rates to assess hypotheses derived from the OGM.

227 *3. Testing hypotheses H1–H3*

228 *H1*. The size and temperature dependence of growth rates from Dataset I were estimated by

229 fitting eqn 2 to log-transformed data,

$$\ln\left[\frac{dm}{dt}\right] = \ln g_o + \gamma \ln m + \frac{E_g}{k}\left(\frac{1}{T_s} - \frac{1}{T}\right) - \ln I(T). \tag{8}$$

9

230 We fit eqn 8 using a Bayesian procedure implemented in the R package *brms* version 2.1.0

231 (Bürkner 2017) in order to derive posterior distributions and associated 95% credible intervals

232 (CIs) for the fitted parameters (Table 1). A hierarchical modeling approach was adopted for

233 this analysis with species-level random effects on the intercept (Supplementary Information).

234 For the analysis of Dataset II, the size and temperature dependencies of optimum growth rates,

235 g_{opt}, at size m_{opt} were estimated by fitting a simplified version of eqn 2, without the inactiva-

236 tion term for the temperature dependence to log-transformed data

$$\ln g_{opt} = \ln g_o + \gamma \ln m_{opt} + \frac{E_g}{k}\left(\frac{1}{T_s} - \frac{1}{T}\right), \tag{9}$$

237 which is equivalent to the simple Boltzmann relationship commonly used in the early

238 Metabolic Theory of Ecology (MTE) literature (Gillooly *et al.* 2002; Brown *et al.* 2004). In

239 contrast to Dataset I, the growth-rate data from Dataset II yielded little evidence of tempera-

240 ture optima (Supplementary Information), most likely because these data were obtained from

241 field-captured individuals, which are not expected to occur above their optimum temperatures

242 in nature. While the lack of well-defined optima provides empirical justification for fitting

243 the simpler Boltzmann relationship to estimate an overall temperature dependence, this

244 approach obscures any changes in temperature dependence over the temperature range. It

245 also results in negative bias for estimated activation energy if a temperature optimum exists.

246 A hierarchical modeling approach was adopted for this analysis, with family-level random

247 effects on the intercept, mass-scaling exponent and temperature-dependence slope ($\Delta\gamma$, ΔE_g,

248 $\Delta\ln g_o$; Supplementary Information).

249 *H2* and *H3*. In Dataset I, we used the paired measurements of metabolic and growth rates to

250 obtain upper-bound estimates for the energy expended in growth, E_m^* (eqn 4), on a wet mass

251 basis. In Dataset II, estimates of E_m (wet mass basis) were calculated using eqn 3 by combin-

252 ing a subset of the g_{opt} estimates ($n = 582$) with estimates of *standard* metabolic rate, which

253 account for the effects of body size and temperature (Barneche *et al.* 2014), and trophic level

254 (Killen *et al.* 2016) (Supplementary Information). In the fish literature, resting rates are re-

255 ferred to as 'standard rates' at some specified temperature because the metabolic rate of a rest-

256 ing fish will vary with ambient temperature. Calculations of E_m were restricted to 13 families

257   with growth rate and standard metabolic rate data. The maintenance-correction term in eqn 3,

258   $[1 - (m_{opt}/M)^{1-\alpha}]$, was assumed to be 0.23 for these calculations, which corresponds to the

259   overall size-scaling exponent for fish resting metabolic rates, $\alpha = 0.77$ (Supplementary Infor-

260   mation).

261   We assessed whether E_m^* (Dataset I) and E_m (Dataset II) exhibit temperature dependence

262   (hypothesis *H2*), and whether E_m (Dataset II only) varies with aspect ratio and trophic level

263   (hypothesis *H3*) by fitting a linear model of the form

$$\ln E_m = \ln\beta_0 + \beta_T T + \beta_L \ln L + \beta_A \ln(A+1), \tag{10}$$

264   where β_0, β_T, β_L, and β_A are respectively the fixed-effect model intercept and three slope pa-

265   rameters, T is temperature in degrees Celsius, L (ranging from 2 to 4.4) is a continuous vari-

266   able for trophic level, and A is the caudal fin aspect ratio (ranging from 0 to 2.99). Species-

267   level estimates of the latter two ecological measures were downloaded from FishBase to as-

268   sess hypothesis *H3* for the E_m estimates in Dataset II. When species values were not available,

269   congeneric species values were used. The relationships of these ecological measures to E_m^*

270   were not investigated for Dataset I because the measures are not representative of trophic level

271   or morphology for individuals at early ontogenetic stages. Model parameters were assigned

272   vague priors in a Bayesian modelling framework. We also included normally distributed ran-

273   dom effects for $\ln\beta_0$ and β_T, thereby allowing them to vary by species (Dataset I) and family

274   (Dataset II). The model fitting procedure in *brms* is similar to that described for eqns 8 and 9

275   (Supplementary Information).

RESULTS AND DISCUSSION

Hypothesis H1

278   The growth rate models (eqns 8 and 9) for both datasets reveal substantial species- (Dataset I)

279   and family-level (Dataset II) variation in size- and temperature-corrected growth rates, charac-

280   terized by standard deviations $\sigma_{\Delta\ln g_o}$. Particularly, the estimate from Dataset I implies a ~1.6-

281   fold change in growth rates among species ($\approx e^{2\times0.22}$, with $\sigma_{\Delta\ln g_o} = 0.22$), while the estimate

282 from Dataset II implies an ~2.2-fold change in growth rates among families ($\approx e^{2 \times 0.39}$, with

283 $\sigma_{\Delta \ln g_o} = 0.39$). After accounting for maintenance costs attributable to age in Dataset II (i.e.

284 $[1 - (m/M)^{1-\alpha}] = [1 - (m_{opt}/M)^{(1-0.77)}] \approx 0.23$), the average estimate of $\ln g_o$ is only about

285 3-fold higher for Dataset I than for Dataset II (Table 1). Therefore, the mass dependencies of

286 growth rates for Datasets I and II can be reasonably approximated by a single allometric func-

287 tion that spans 10 orders of magnitude in body mass (Fig. 1).

288   Contrary to hypothesis *H1*, the analyses of Datasets I and II yield contrasting estimates for

289 the mass scaling of growth rates, characterized by the scaling exponent γ (Table 1). The av-

290 erage within-species γ is significantly steeper than 0.75 early in ontogeny (Dataset I average:

291 0.85; 95% CI: 0.80–0.91), but statistically indistinguishable from 0.75 at the size of optimum

292 growth rate (Dataset II average: 0.77; 95% CI: 0.74–0.80). It is possible that the true scaling

293 exponent in Dataset I would approach a value of 1 (i.e. isometric mass scaling) if variation

294 in energy allocation to maintenance with ontogenetic stage, m/M, were accounted for. One

295 would need full ontogenetic growth trajectories for these individuals (as we have for Dataset

296 II) – including asymptotic adult mass, which can vary with temperature and other factors – in

297 order to estimate their maintenance costs.

298   Overall, our results are consistent with previous observations that metabolic scaling is

299 steeper early in ontogeny for fish (e.g. Bochdansky & Leggett 2001). They also highlight the

300 importance of correction for ontogeny in order to properly evaluate mass scaling of growth

301 rates among species (Moses *et al.* 2008), and reinforce the idea that the scaling of biological

302 rates early in ontogeny may be steeper than the canonical value of 3/4 that is generally as-

303 sumed by MTE (West *et al.* 1997), perhaps due to changes in the circulatory system during

304 larval-post larval transition. The model of West *et al.* (1997), in fact, predicts positive de-

305 viations from 3/4-power scaling if size range encompasses very small organisms that have

306 vascular distribution networks with only a few levels of branching. Evaluating more detailed

307 predictions would require data on aorta and capillary diameters, and the numbers of branching

308 generations from aorta to capillary (West *et al.* 1997, 2001; Brummer *et al.* 2017).

309 *Hypotheses H2–H3*

310 The average temperature dependence of growth rates differ between Datasets I and II. While

311 it is statistically indistinguishable from the predicted 0.6–0.7 eV range for Dataset I (average

312 for E_g: 0.65 eV; 95% CI: 0.48–0.93 eV), consistent with previous estimates of temperature

313 dependence of developmental times in fishes (Pauly & Pullin 1988; Gillooly *et al.* 2002), it is

314 significantly shallower than this value for Dataset II (average for E_g: 0.26 eV; 95% CI: 0.19–

315 0.34 eV). This unexpected low temperature dependence might be due in part to errors in age

316 estimation in seasonally-growing species (Campana 2001), statistical artifact of errors intro-

317 duced by estimating masses from length-weight functions, and/or negative bias for the esti-

318 mated activation energy due to our inability to account for temperature optima. It might also

319 reflect differences in how laboratory-grown (Dataset I) versus field-grown (Dataset II) fish re-

320 spond to temperature, perhaps owing to (*i*) differences in resource availability, or (*ii*) changes

321 over ontogeny.

322   Estimates of E_m^* and E_m cover a similar range of values, and vary by ~3 orders of magni-

323 tude (Fig. 2). While these estimates highlight substantial variation in the calculated amount of

324 energy an organism must expend in producing biomass, we note that they are comparable in

325 magnitude to values reported for other groups of animals including insects, bivalves, anurans,

326 birds and mammals (Wieser 1994; Moses *et al.* 2008; Sears *et al.* 2012).

327   Consistent with hypothesis *H2*, the estimated upper-bound E_m^* was independent of tem-

328 perature in 78% of the 18 species in Dataset I (i.e. 95% credible intervals overlapped 0; β_T

329 = -0.04, 95% CI: -0.08–0.01; Fig. 2). In contrast, we observed a significant temperature de-

330 pendence of E_m in 92% of the 13 families for which we could calculate E_m in Dataset II, with

331 an average 22-fold increase in E_m moving from 0˚C to 30˚C (β_T = 0.1032, 95% CI: 0.0701–

332 0.1411; Fig. 2). Thus, these results suggest that a fish in the tropics requires substantially

333 more assimilated energy to produce a unit of biomass than a fish in the polar regions. The dis-

334 crepancy we observe with regard to temperature dependence for E_m between Datasets I and II

335 warrants further investigation and careful scrutiny. Given this important caveat, our results for

336 Dataset II are consistent with earlier accounts of decreasing growth efficiency with increasing

337 temperature in fishes (e.g. Houde 1989; Jobling 1997; McCarthy *et al.* 1998) and microbes

338 (Apple *et al.* 2006).

339   After accounting for the effects of temperature, contrary to hypothesis *H3*, we found sub-

340 stantial evidence (i.e. 95% posterior credible intervals did not overlap 0) of systematic in-

341 creases in E_m with fish trophic level ($\beta_L = 0.73$, 95% CI: 0.34–1.12), and aspect ratio ($\beta_A =$

342 0.41, 95% CI: 0.10–0.71). Therefore, our results are consistent with the fact that species with

343 higher muscle protein content might exhibit higher metabolic costs to build biomass. How-

344 ever, top predators may have higher assimilation efficiencies (Sanders *et al.* 2016). Thus, our

345 findings may reveal some important physiological trade-offs (i.e. assimilation efficiency ver-

346 sus cost of growth) that might occur across trophic levels, which will have fundamental effects

347 on the trophic structure of food webs (see below).

348 *The role of E_m in constraining trophic efficiency and food-web structure*

349   We integrated the assimilation rate numerically in eqn 6 to calculate the curves for Fig. 3.

350 Results of these calculations demonstrate that the efficiency of energy transfer varies consider-

351 ably with E_m over the range of values that were empirically observed in Fig. 2. In fact, the ef-

352 fects of E_m are of comparable magnitude to those of ontogenetic stage, highlighting the quan-

353 titative importance of this variable for understanding energy transfers between trophic levels.

354 Moreover, eqn 6 also predicts that higher values of activity scope (f) will have substantial

355 negative effects on the efficiency of energy transfer, highlighting the ecological importance

356 that this variable has to food-web trophic structure (Killen *et al.* 2016).

357   The calculated range of efficiencies depicted in Fig. 3 were combined with parameters

358 from eqn 7 in order to predict how ecosystem-level size structure may change in relation to

359 prey growth energetics, E_m, and ontogenetic stage, m/M (Fig. 4). For instance, our model

360 indicates that the existence of real closed-system top-heavy pyramids may be energetically

361 and ecologically unlikely (e.g. Trebilco *et al.* 2016) – red area in Fig. 4 – because individu-

362 als would need to be characterized by low values of E_m, and would have to prey exclusively

363 on very young offspring (i.e. high-efficiency prey resource). Moreover, compared to aquatic

364 food-webs where the youngest prey available are comprised of eggs and larvae (i.e. $m/M \approx$

365 0), communities of viviparous animals (e.g. mammals with large offspring relative to adult

366 size), might be constrained to have a bottom-heavy trophic pyramid at least in part because the

367 youngest prey items available (e.g. newborn cubs) are relatively large relative to their asymp-

368 totic size and thus relatively inefficient at accruing biomass after birth. Future refinement and

369 tests of these predictions will require an assessment of ontogenetic stage of prey items in diets

370 of different species at the community level.

371   Our approach builds on a simple static size spectrum model (Brown & Gillooly 2003), but

372 could inform more sophisticated contemporary dynamic size spectrum models that explicitly

373 connect ontogenetic growth to population and ecosystem dynamics (e.g. Andersen *et al.* 2016;

374 Blanchard *et al.* 2017). For example, these models incorporate ontogenetic growth in a man-

375 ner that is more closely related to the BGM. Recognizing that the efficiency of energy transfer

376 changes with the relative ontogenetic stage of the prey, and that this efficiency might change

377 with temperature, trophic and activity levels through their effects on E_m (but see Barange *et al.*

378 2014 for recent integration of temperature effects) may therefore represent a fundamental step

379 forward.

380   Finally, our findings might also yield important insights in terms of fisheries management.

381 For example, in oligotrophic coastal marine communities such as coral reefs, mass-spawning

382 events are very frequent (e.g. Harrison *et al.* 1984), and high-efficiency recycling of energy

383 and nutrients might be imperative. Thus, preserving large individuals that produce more (and

384 larger) eggs in aquatic communities (Birkeland & Dayton 2005) may be key to the mainte-

385 nance of high-efficiency energy transfers between trophic levels. Understanding the energetics

386 of growth across different trophic levels (and/or functional groups) might therefore help estab-

387 lish baselines of recovery potential in coastal fisheries (MacNeil *et al.* 2015).

388 **FUTURE DIRECTIONS**

389 Overall, our study demonstrates how growth rate and metabolic rate data can be synthesized

390 within a theoretical framework to obtain a deeper understanding of the energetics of growth

391 (Fig. 1). Particularly, our results reveal fundamental constraints (Fig. 2) on ecosystem dynam-

392 ics that arise from individual-level metabolism (Figs. 3 and 4). Our analysis highlight general

393 trends, but also important differences among datasets, as well as among species, particularly

394 with regards to the temperature dependence of E_m. New methods are needed to quantify and

395 predict E_m – across a broad range of taxa in both terrestrial and aquatic systems – based on the

396 underlying energetics of the biochemical processes involved in the construction of biomass.

397 Uncovering the drivers of variation in this single quantity (e.g. temperature, mode of activity,

398 habitat, phylum) is a fruitful avenue forward: it offers an opportunity to bridge multiple dis-

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ciplines – from physiology to phylogenetics to ecosystem ecology – across space and time. Such an interdisciplinary approach is needed if we are to predict how rising temperatures are going to affect life-history evolution, ecosystem dynamics, the rehabilitation of economically important fisheries stocks, and the global carbon cycle.

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TABLES

Table 1. Point estimates and 95% credible intervals (as determined using Bayesian methods) for fitted parameters in the growth rate models. Fixed-effect parameters include: γ, the average for the mass-dependence of growth rate; E_g, the average for the temperature dependence of growth rate; $\ln g_o$, the average for the mass-corrected growth rate at temperature T_s = 15˚C; T_{opt} (Dataset I only), the temperature optimum of fish growth rates and E_i (Dataset I only), the inactivation parameter describing the rate of decline in growth rate at temperatures $> T_{opt}$. Random-effects include the standard deviations for species- (Dataset I) and family-level (Dataset II) variation in size- and temperature-corrected rates at T_s ($\Delta \ln g_o$) as well as standard deviation for family-level size dependence ($\Delta \gamma$) and temperature dependence ΔE_g (Dataset II only).

Parameter	I			II		
	Mean	**2.5%**	**97.5%**	**Mean**	**2.5%**	**97.5%**
Fixed Effects						
Mass, γ	0.85	0.80	0.91	0.77	0.74	0.80
Activation energy, E_g (eV)	0.65	0.48	0.93	0.26	0.19	0.34
Inactivation parameter, E_i (eV)	2.67	1.18	4.74			
Optimum temperature, T_{opt} (K)	302.47	296.91	309.69			
Normalization, $\ln g_o$ (g g$^{-\gamma}$ d^{-1})	-3.04	-3.38	-2.57	-5.52	-5.67	-5.34
Random effects						
Std. Deviation of $\Delta \ln g_o$	0.22	0.04	0.47	0.39	0.20	0.61
Std. Deviation of $\Delta \gamma$				0.07	0.04	0.11
Std. Deviation of ΔE_g				0.24	0.17	0.32
Correlation of $\Delta \ln g_o$ and $\Delta \gamma$				-0.70	-0.90	-0.28
Correlation of $\Delta \ln g_o$ and E_g				0.04	-0.43	0.53
Correlation of $\Delta \gamma$ and ΔE_g				0.08	-0.34	0.49

21

FIGURE LEGENDS

Figure 1. Scaling of growth rates of fish with respect to (left) body mass and (right) and temperature in Datasets I (white squares) and II (grey circles). Parameter estimates (listed in Table 1) were obtained using Bayesian methods. The effect of temperature on growth rate was controlled for by standardizing the temperature measures, T (in K), to $T_s = 288.15$ K ($= 15°C$) based on temperature scaling relationships, where k is the Boltzmann constant (8.62×10^{-5} eV K^{-1}). The effect of body mass was controlled for by standardizing measures to 1 gram based on the mass scaling relationships. The mass-corrected rates at temperature T_s, $\ln g_o$, for Dataset I (-3.04 g$^{1-\gamma}$ d^{-1}) and Dataset II (-5.52 g$^{1-\gamma}$ d^{-1}), correspond to averages across species and families, respectively. Dataset I was fitted to a model that allowed $\ln g_o$ to vary among species, whereas Dataset II was fitted to a model that allowed $\ln g_o$, γ, and E_r to vary among families. Growth rates from Dataset II are optimum growth rates (g_{opt}) and mass is mass at optimum growth rates (m_{opt}). Thus, the ontogenetic stage was controlled for (eqn 1) by expressing growth rates as $(dm/dt)[1 - (m/M)^{1-\alpha}]$, assuming $[1 - (m/M)^{1-\alpha}] = 0.23$ for Dataset II. For Dataset I, it was assumed that $[1 - (m/M)^{1-\alpha}] = 1$ because growth rates were measured at an early ontogenetic stage.

Figure 2. Distributions of values for E_m (in J g^{-1} wet mass), the amount of energy necessary to produce a unit of biomass at both embryo/larval growth rate (white squares, Dataset I), and maximum growth rate (grey circles, Dataset II). Values from Dataset I are upper-bound estimates of E_m^* obtained from 179 direct measurements of growth rates and metabolic rates (assuming $[1 - (m/M)^{1-\alpha}] = 1$, eqn 4). Values from Dataset II are E_m estimates (eqn 3) calculated for 582 growth-rate measurements, which encompass 13 families that overlap with the standard metabolic-rate data from FishBase (Barneche *et al.* 2014). Equations in the top-left represent the fixed-effect estimates of the temperature dependence of E_m^* and E_m for Datasets I and II, respectively.

Figure 3. Upper-bound estimates for the efficiency of energy transfer given different values for ontogenetic stages, m/M, and E_m (J g^{-1}) (eqns 1, 3, 4, 5 and 6). Efficiencies only incorporate energy losses due to respiration, and thus exclude losses attributable to other processes. Polygons were calculated for different values of E_m (wet mass basis) which encompass the

567   range of values estimated in Fig. 2, assuming that $m_o = 0$ g, $\alpha = 0.77$, $B_o = 18.67$ J g$^{-0.77}$ d^{-1}

568   for fish at 15˚C (Table S1), and $E_c = $ (24 kJ g^{-1} dry mass) (0.15 g dry mass g^{-1} wet mass) =

569   3,600 J g^{-1} wet mass (Hou *et al.* 2008). Polygon upper and lower bounds represent the effi-

570   ciencies of individuals either at permanent resting ($f = 1$) or active ($f = 4$) state. An average f

571   = 4 is consistent with evidence reported for fishes (Killen *et al.* 2016). The values for m (size

572   at the time of consumption) and M (asymptotic adult size of the prey individual) are arbitrary

573   because ε depends only on their ratio.

574   **Figure 4.** Relationship between ontogenetic stage of prey at time of predation and energy nec-

575   essary to produce a unit of biomass E_m, and the resulting effects on the size structuring of bi-

576   ological communities and the energy transfer efficiency between trophic levels (ε, eqns 5, 6

577   and 7). Different colors indicate different resulting community biomass (W) – individual body

578   mass (m) scaling relationships, with blue areas depicting bottom-heavy pyramids and red areas

579   depicting top-heavy pyramids. The black solid line represents an area where $W \propto m^0$, i.e. a

580   biomass stack, which corresponds to an average energy transfer efficiency of 0.14. The values

581   in the figure were calculated assuming $PPMR = 2327{:}1$ (following Al-Habsi *et al.* 2008), $\alpha =$

582   0.77, and $f = 2.4$ in eqn 5.