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1 **Title**

2 Multiple working hypotheses for hyperallometric reproduction in fishes under  
3 metabolic theory

4  
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12

13 **Keywords**

14 Fishes, Dynamic Energy Budget, Scaling, Life history, Variability

15

16 **Abstract**

17 Hyperallometric reproduction, whereby large females contribute relatively more  
18 to the renewal of the population than small females, is purported to be  
19 widespread in wild populations, especially in fish species. Bioenergetic models  
20 derived from a sufficiently general metabolic theory should be able to capture  
21 such a relationship but it was recently stated that no existing models adequately  
22 capture hyperallometric reproduction. If this were true it would seriously  
23 challenge our capacity to develop robust predictions of the life history and  
24 population dynamics in changing environments for many species. Here, using the  
25 European sea bass (*Dicentrarchus labrax*) as a test case, we demonstrate  
26 multiple ways that hyperallometric reproduction in a population may emerge  
27 from the Dynamic Energy Budget (DEB) theory, some inherently related to the  
28 metabolism and life history and others related to plastic or genetically based  
29 intraspecific variation. In addition, we demonstrate an empirical and modelled  
30 hypoallometric scaling of reproduction in this species when environment is  
31 controlled. This work shows how complex metabolic responses may underlie  
32 apparently simple relationships between weight and reproduction in the wild

33 and provides new and testable hypotheses regarding the factors driving  
34 reproductive scaling relationships found in the wild.

35

## 36 **INTRODUCTION**

37 Hyperallometric reproduction, defined as a more than proportional increase of  
38 the fecundity relative to the body mass of individuals within a species, has a wide  
39 range of consequences for our understanding of population dynamics, our  
40 predictions in a changing environment and ultimately our conservation policies  
41 (Marshall et al., 2019). Such a reproductive scaling pattern has recently been  
42 described for a wide range of fish species (Barneche et al., 2018) and implies that  
43 large females contribute more to the renewal of the population than do small  
44 females, relatively to their body mass. Large females therefore have a higher  
45 conservation value and their protection should be prioritized over small females  
46 to increase the sustainability of the population (Birkeland and Dayton, 2005).

47

48 Ideally, population dynamics models should be driven by an underlying model of  
49 bioenergetic processes that can explicitly capture the observed scaling of  
50 reproduction. A number of 'growth models' now exist, including some derived  
51 from general theories of how metabolism works, i.e. 'metabolic theories' (van der  
52 Meer, 2006). It was recently argued that the observed hyperallometric scaling of  
53 reproduction could not be explained using current bioenergetic models  
54 (Marshall and White, 2019). If this were true, and hyperallometric reproduction  
55 is indeed widespread, it would call into question the generality of existing theory  
56 and limit our capacity to develop robust models of the life history and population  
57 dynamics for many species.

58

59 However, a pattern of hyperallometric reproduction observed in wild  
60 populations is challenging to interpret when the age, environmental life history  
61 and genetic background of the individuals displaying this relationship are  
62 unknown (Kearney 2019). This is the case for the data underlying  
63 hyperallometric reproduction in fish which derive almost entirely (>98%) from  
64 observations of wild individuals (Barneche et al., 2018). Investigating a fecundity  
65 to body mass scaling naturally results from the comparison of different sized

66 individuals. But what is driving this variability? Why are large individuals larger?

67 Multiple biological explanations are possible.

68

69 First, in nature, there is no reason to believe that all animals encounter the same  
70 environmental conditions over their life history. This is particularly true for  
71 species with wide geographical and habitat ranges (Riede, 2004; Wheeler, 1975),  
72 including the Atlantic cod and European sea bass. Comparing the weight and  
73 reproductive output of wild-harvested individuals of such species necessarily  
74 involves confounding effects related to environmental history. These effects are  
75 amplified when investigating the variability in weight without evaluating the age,  
76 since large animals are more likely to have encountered better environments  
77 compared to small individuals of the same age.

78

79 Second, whether it is the consequence of predation, of sudden environmental  
80 challenges or of human activities, selective pressures in the wild are particularly  
81 numerous and diversified. These multiple sources of selection are considered as  
82 the primary mechanisms of polymorphism in nature (Orr and Smith, 1998).

83 Metabolic capacities driving growth, maturation, reproduction and ultimately  
84 fitness are central phenotypic targets of selective pressures (Pettersen et al.,  
85 2018). Within a given population, one can expect genetically based variability in  
86 metabolic capacities resulting in intrinsic individual differences in assimilation  
87 and growth capacity (Besson et al., 2019). Thus, the life history patterns  
88 obtained from wild-harvested individuals may also reflect the action of selection.

89

90 The environmental and genetic variation inherent in samples from wild  
91 populations means that one should be cautious in attributing a pattern of  
92 reproductive hyperallometry to metabolic mechanisms involved at the  
93 individual level. Rather than using such an empirical observation to dismiss  
94 existing models of individual growth and metabolism, one can instead ask under  
95 what environmental and genetic circumstances the model would produce the  
96 empirical pattern in question. This then leads to clear and testable predictions  
97 about what might be occurring in nature. In parallel, detailed laboratory

98 experiments are critical to control and evaluate selective pressures and  
99 environmental variabilities and thereby evaluate theoretical expectations.

100

101 A common point of contention and misunderstanding in modelling growth  
102 centers around the distinction between phenomenological and mechanistic  
103 models (White and Marshall, 2019). A phenomenological model provides a  
104 quantitative description of a process using a simple function thought to capture  
105 the essence of an underlying process; often these are allometric functions in the  
106 case of growth models. In contrast, mechanistic models are derived through the  
107 explicit representation of processes occurring at a lower level to the  
108 phenomenon in question. In growth models, these processes are the chemical  
109 transformations from food to biomass, which are modelled on the basis of  
110 physicochemical principles including energy and mass conservation. Successful  
111 mechanistic models can predict dynamics under complex sequences of  
112 environmental conditions with the same variables and parameters – something  
113 phenomenological models cannot do without adding parameters or changing  
114 their functional form. In this sense, mechanistic modeling can help reconstruct  
115 environmental history when they are inverted to fit growth data from the wild  
116 (Lavaud et al., 2019; Pecquerie et al., 2009).

117

118 In this paper, we explore the potential for reproductive hyperallometry under  
119 the framework of Dynamic Energy Budget (DEB) theory; a general, mechanistic  
120 metabolic theory that captures the environmental (food, temperature) and  
121 internal (chemical transformations and allocations) constraints on development,  
122 growth and reproduction from first principles (Kooijman, 2010, 1986). In  
123 particular, we consider three working hypotheses (Figure 1) and illustrate them  
124 using the European sea bass, *Dicentrarchus labrax*, a species shown to exhibit  
125 hyperallometric reproduction in the wild (Mayer et al., 1990):

126

127 1) the 'ontogenetic hypothesis' that hyperallometric reproduction can emerge  
128 for an individual simulated under DEB theory across its ontogeny;

129

130 2) the ‘environmental variation hypothesis’ that hyperallometric reproduction  
131 can be produced by realistic variation in feeding rate and temperature  
132 environments among individuals with the same metabolic capacities;

133

134 3) the ‘metabolic capacities variation hypothesis’ that inter-individual variation  
135 in DEB parameter values can lead to hyperallometric reproduction.

136

137 Finally, we provide empirical data on the allometric scaling of reproduction  
138 under controlled environmental conditions and limited selection pressure. We  
139 discuss our results in the light of DEB predictions under such environmental  
140 conditions. Since the DEB model is generic between fish species (only  
141 parameters vary), the results of our study are transposable to most other fish  
142 species.

143

144

## 145 **METHOD**

146 *The DEB model for D. labrax*

147 The DEB parameters for *D. labrax* used in our simulations are available online  
148 (Lika et al., 2018) and are provided in Supplementary tables 1, 2 and 3. They  
149 were inversely estimated from observations on development times (at multiple  
150 temperatures), lengths and weights at birth/hatch, metamorphosis, maturation  
151 and ultimate size as well as growth curves in length and weight, reproduction  
152 and feeding rate vs. weight and ammonia production vs. temperature  
153 (Stavrakidis-Zachou et al., 2019). The one-to-many relationship between  
154 parameter values and expected observations in the estimation procedure,  
155 together with the requirement for physically permissible parameter values (e.g.  
156 not violating mass or energy conservation) strongly constrains the possible  
157 parameter values.

158

159 The standard DEB model considers the organism to be made up of two  
160 macrochemical pools of fixed stoichiometry, the ‘reserve’  $E$  and ‘structure’ ( $V$ )  
161 which, together with the maturity state  $E_H$  and the reproduction buffer  $E_R$ ,  
162 comprise the state variables of the model as depicted by the 4 compartments in

163 Figure 2 (Kooijman, 2010). The theory assumes that an organism transforms  
164 food into a reserve compartment at a daily rate  $\dot{p}_A$  (Supplementary table 4)  
165 proportional to its structural surface ( $V^{2/3}$ ), the scaled functional response ( $f$ )  
166 and the DEB parameter  $\{\dot{p}_{Am}\}$ . The  $f$  value is expressed as a fraction of the  
167 maximum possible feeding rate and therefore takes values between 0  
168 (starvation) and 1 (feeding *ad libitum*). Energy is then mobilized from the  
169 reserve compartment at a rate  $\dot{p}_C$  under 1<sup>st</sup> order dynamics (Figure 2,  
170 Supplementary table 4). A fraction ( $\kappa$ ) of this energy contributes to growth ( $\dot{p}_G$ )  
171 after having paid for the maintenance of the structure ( $\dot{p}_S$ , proportional to  
172 structural volume  $V$ ), while  $1 - \kappa$  goes to maturation ( $\dot{p}_R$ ) and its associated  
173 maintenance ( $\dot{p}_J$ ). The standard DEB model assumes that  $\kappa$  remains constant  
174 throughout the life-cycle of the animal, consistent with the close fit of the  
175 Pütter/von Bertalanffy growth model to empirical data (Kooijman, 2010).  
176 Maturity is achieved when total energy invested in maturation reaches  $E_H^p$   
177 (Supplementary table 1). Then,  $\dot{p}_R$  becomes the amount of energy invested daily  
178 in reproduction (Figure 2). The model uses nine parameters (Supplementary  
179 table 1) to calculate these six energy fluxes ( $\dot{p}_A$ ,  $\dot{p}_C$ ,  $\dot{p}_S$ ,  $\dot{p}_J$ ,  $\dot{p}_G$  and  $\dot{p}_R$ ) following the  
180 standard DEB model (Kooijman, 2010). In addition, five parameters  
181 (Supplementary table 2) are used for the calculation of the thermal correction  
182 coefficient (Supplementary table 4) which modulates energy fluxes by  
183 temperature.

184

185 The DEB model for *D. labrax* assumes a metabolic acceleration between hatching  
186 and a transition phase called “metamorphosis” (Kooijman, 2014). This  
187 acceleration, common in fish species (Kooijman et al., 2011), consists of a period  
188 where growth is not isometric but, instead, growth in structural surface is  
189 proportional to the growth of structural volume ( $V$ ) (Supplementary table 4).  
190 Acceleration ends when the amount of energy invested in maturation reaches  $E_H^j$   
191 (Supplementary table 1). At a given time, an organism is described by its stored  
192 reserves ( $E$ ), structural volume ( $V$ ), maturity ( $E_H$ ) and reproductive buffer ( $E_R$ ).  
193 The dynamics of  $E$ ,  $L$ ,  $E_H$  and  $E_R$ , and the associated metabolic processes are  
194 presented in the Supplementary table 4.

195 We estimated the wet weight as the sum of stored reserves and total soma,  
196 assuming a water content of 80% (Supplementary table 4). In contrast to  
197 Kearney (2019), we excluded reproduction buffer from the weight calculation,  
198 instead modeling the weight of a female post spawning. No reproduction buffer  
199 handling rule was used since the total reproductive buffer was not affecting the  
200 total weight nor the daily investment in reproduction in our simulations.

201

### 202 *Simulations based on our 3 hypotheses*

203 The DEB model was run for *D. labrax* at a body temperature of 19°C and a  
204 feeding rate set at 70% of the satiety. While keeping all parameters equal across  
205 all simulations, only one forcing variable (temperature or feeding rate) or one  
206 target DEB parameter (see below) was modified according to the hypothesis  
207 being explored (Figure 1).

208 To test the ‘ontogenetic hypothesis’, reproductive output and weight over  
209 several ages post maturity were compared for the average *D. labrax* living at  
210 19°C and a 70% feeding rate. To assess the ‘environmental variation’ hypothesis,  
211 weight and reproductive output of the animals were compared at 2000 days post  
212 fertilization (dpf) and we tested the effects of:

- 213 - Differences in whole-life-cycle body temperature from 15 to 23 °C in 2 °C  
214 intervals, with a 70% feeding rate.
- 215 - Differences in feeding rate, ranging from 60 to 80% of maximum feeding  
216 rate and body temperature at 19°C.

217

218 Similarly, the ‘metabolic capacities variation’ hypothesis was tested on  
219 simulations performed at 19°C and 70% feeding rate and data were compared at  
220 2000 dpf for individuals varying in one DEB parameter at a time. The effects of a  
221 variation from -10 to +10% around the average value available for *D. labrax*  
222 (Lika et al., 2018) was evaluated. We tested all parameters of Supplementary  
223 table 1 leading to a significant change in weight and reproductive investment at a  
224 given age and therefore focused on the following parameters:

- 225 - The “surface-area-specific maximum assimilation rate” ( $\{p_{Am}\}$ , in  
226 J/d/cm<sup>2</sup>), driving the maximum amount of energy the animal can  
227 assimilate per unit of structural surface when food is *ad libitum*.



- 228 - The “allocation fraction to soma” ( $\kappa$ ), specifying the fraction of energy  
229 mobilized from the reserve compartment allocated to the production and  
230 maintenance of structure.
- 231 - The “specific cost for structure” ( $[E_G]$ , J/cm<sup>3</sup>), which represents the cost  
232 (biomass and overhead) to the animal of transforming the energy  
233 allocated towards growth ( $\dot{p}_G$ ) in structure.
- 234 - The “somatic maintenance cost” ( $[\dot{p}_M]$ , J/cm<sup>3</sup>/d), corresponding to energy  
235 requirements to maintain a unit of structure.
- 236 - The “maturity at birth” ( $E_H^b$ ), the amount of energy invested in maturation  
237 needed to start feeding (considered as birth).
- 238 - The “maturity at metamorphosis” ( $E_H^j$ ), the amount of energy invested in  
239 maturation needed to finish the acceleration phase.

240

#### 241 *Testing hypo-, iso- or hyperallometry*

242 Hyperallometry was tested by comparing DEB model outputs for wet weight and  
243 daily investment in reproduction on log<sub>10</sub> transformed axes. A linear model was  
244 fitted to the simulated data and the hypothesis of hyperallometry was accepted if  
245 the model slope was higher than one (Figure 1). A scaling with a slope of one is  
246 considered isometric while a slope below one is called hypoallometric (Barneche  
247 et al., 2018).

248

#### 249 *Empirical test of reproductive scaling*

250 An empirical test of hyperallometric reproduction was based on weight and total  
251 reproductive volume data available for *D. labrax*, from the research center in  
252 Palavas (Ifremer). In this research center, animals were reared in identical  
253 environmental conditions at densities below 30kg/m<sup>3</sup> and selective pressure  
254 during the rearing was lowered as much as possible to maximize survival. Tanks  
255 were supplied with seawater at a temperature ranging from 13 to 25 °C, with an  
256 average of 18.01 °C between years 2012 and 2019. Oxygen concentration was  
257 maintained between 90 and 120% saturation, via oxygen supplementation. Fish  
258 were reared under natural light and fed on-demand with a commercial diet using  
259 a self-feeder with a limit of 1% of the total biomass per day, five days per week.  
260 During the breeding season (starting in January), females, weighing 3.3kg ± 1.5

261 S.D., at a near spawning stage were hormonally injected and the total volume  
262 spawn was measured. The daily investment in reproduction was estimated over  
263 time using the DEB model with a feeding rate of 71.4% (corresponding to a  
264 feeding frequency of 5 days per week) and a temperature of 18 °C, and compared  
265 against the weights measured in the empirical test.

266

## 267 **RESULTS**

268

269 Figure 3 summarizes the outcomes of DEB simulations leading to hypo-, iso- or  
270 hyper-allometric reproduction, as a result of our three working hypotheses.

271

### 272 *Ontogenetic Hypothesis*

273 The DEB model parameters for European sea bass generated a close to isometric  
274 scaling of reproduction under a constant environment from sexual maturity to  
275 10000 days post fertilization (dpf) (Figure 3A). This suggests that investment in  
276 reproduction relative to body mass is constant overtime. Thus, the daily  
277 reproductive investment per body mass of the biggest female of the simulation  
278 (10000 dpf, 2151g) was comparable to that of the smallest (1200 dpf, 659g),  
279 with 7.87 and 7.5 J/g wet weight respectively. Nevertheless, between these two  
280 extreme points, the scaling was not linear, and the pattern observed in  
281 reproductive scaling depended on whether younger or older classes of fish were  
282 studied, i.e. it varied with ontogeny. If only younger fish (less than 2000 dpf, and  
283 1324g) were used for the relationship, the scaling became hyperallometric (red  
284 line in Figure 3A). On the contrary, when the scaling was investigated for older  
285 individuals, hyperallometry was lost and the relationship even became  
286 hypoallometric (blue line in Figure 3A).

287

### 288 *Environmental Variation Hypothesis*

289 Within the temperature range investigated here (15 to 23 °C), increasing  
290 temperature led to heavier fish at a same age, purely due to the rate effects of  
291 temperature on growth (Figure 3B). These fish also invested more in  
292 reproduction, and this effect increased disproportionately with body mass. An  
293 exponent of almost 2 (1.97) was found for this thermal range. This translates to

294 an investment in reproduction relative to body mass two times (5.33 vs 11.65 J/g  
295 wet weight) greater for the biggest fish of the simulation compared to the  
296 smallest (806 vs 1778g).

297 Growth and reproduction were also strongly positively influenced by the feeding  
298 rate (Figure 3B). Between-individual variability in feeding rate over the range  
299 considered (60 to 80%) also led to an apparent hyperallometry in the  
300 relationship for *D. labrax*, with an exponent of 1.34 (Figure 3B). The females  
301 having assimilated more energy during their life history were heavier, but they  
302 also invested more in reproduction than small females relative to their body  
303 mass.

304

#### 305 *Metabolic Capacities Variation Hypothesis*

306 In DEB theory, variability in metabolic capacities among individuals translates to  
307 variability in DEB parameters. Allowing DEB parameters to vary individually  
308 around their estimated values (Lika et al., 2018) can lead to apparent hypo-, iso-  
309 or hyper-metric reproduction (Figure 3C). This was observed when comparing  
310 individuals of the same age (here 2000 dpf) with an identical environmental life  
311 history but varying some of their intrinsic metabolic capacities (Figure 3C). A  
312 variability ranging from -10 to +10% in the relative allocation to reproduction  
313 ( $\kappa$ ) can show strong hypoallometry (Figure 3C). With an increase of  $\kappa$ , weight  
314 rose but less energy was invested in reproduction. Individuals with higher  $\kappa$   
315 allocated more energy towards structure and therefore grew faster (Figure 2). In  
316 parallel, a lower fraction ( $1 - \kappa$ ) of the energy was available for reproduction,  
317 leading to shortened daily investment in reproduction. Females with lower  $[E_G]$   
318 became larger at a same age, but they invested the same amount of energy in  
319 reproduction proportionally to their body mass, leading to isometric scaling.  
320 Indeed, a change in  $[E_G]$  affects only the final transformation of energy to volume  
321 of the structure. On the contrary, a change in  $\{\dot{p}_{Am}\}$  resulted in hyperallometric  
322 relationship (Figure 3C) in accordance with changes in feeding rate, both  
323 involved proportionally in the same DEB equation (See calculation of the  
324 assimilation rate,  $\dot{p}_A$ , in Supplementary table 4). A change in maturity thresholds  
325  $E_H^b$  and  $E_H^j$  also resulted in hyperallometric reproduction (Supplementary Figure  
326 1). The decrease of  $E_H^b$  or the increase of  $E_H^j$ , led to increased weight and energy

327 invested in reproduction for *D. labrax* of the same age. The increase was  
328 nevertheless disproportionate, with large individuals investing more than small  
329 individuals relative to body mass.

330

#### 331 *Empirical scaling in controlled conditions*

332 Our laboratory data on reproductive scaling for weights ranging from 0.5 to 10  
333 kg under constant food and temperature show that *D. labrax* displayed a  
334 hypoallometric scaling of reproduction (Figure 3A). The DEB model for *D. labrax*  
335 run using the ontogenetic hypothesis (weight differences are the result of age  
336 differences) on the same empirical weights predicted a similar hypoallometric  
337 reproduction (Figure 3B). The exponents extracted from empirical and  
338 simulated scalings were comparable (0.843 vs 0.888 respectively).

339

## 340 **DISCUSSION**

341

342 Collectively, our results demonstrate that multiple biological explanations  
343 integrated in DEB simulations can lead to the hyperallometric reproduction  
344 previously observed for a wide range of fish species in the wild (Barneche et al.,  
345 2018). DEB models have been used to capture the life cycle of more than 2000  
346 animal species across all major phyla; our results are therefore likely applicable  
347 to many other species (Kooijman et al., 2020). We thus show that it is premature  
348 to conclude that patterns of hyperallometric reproduction in nature necessitate a  
349 major revision of all existing growth models (Marshall and White, 2019).

350

351 Moreover, our empirical data on *D. labrax* obtained in controlled conditions are  
352 not consistent with the hyperallometric pattern seen in wild fish. This striking  
353 contrast probably derives from the differences between wild and laboratory  
354 conditions. Wild caught animals are necessarily more varied in their  
355 environmental life histories or intrinsic metabolic capacities than their  
356 counterpart laboratory reared animals. Consequently, laboratory conditions  
357 permit more powerful tests of ontogenetic scaling relationships because  
358 temperature, food availability and water quality can be controlled. In addition,

359 selective pressure is relaxed, reducing the selection based on growth, maturation  
360 or reproduction for all animals of the population.

361

362 It is surprising that so few laboratory data are available on the scaling of fish  
363 reproduction. Yet laboratory settings may also impose confounding factors. For  
364 instance, spawning in our laboratory study was induced by hormonal injection  
365 (Ako et al., 1994; Emata, 2003) and we do not know whether this could influence  
366 the allometric pattern. However, assuming a concentration of 905 eggs per mL  
367 (Chatain, 1994), our empirical data fall (mean = 150 118 +- 58 800 eggs/kg) in  
368 the range of non-induced spawning in European sea bass (Cerdá et al., 1995).

369

370 Our DEB simulations run using the empirical environmental conditions under  
371 the ontogenetic hypothesis, where the weight of individuals was only differing  
372 according to age, were very good at predicting the empiric hypoallometric  
373 scaling observed. This hypoallometric reproduction was also observed in Figure  
374 3A on the heaviest (and oldest) animals, with a weight starting at 1324g. The  
375 females from the Ifremer Research Station of Palavas used for the scaling, were  
376 much heavier (mean above 3000g), leading to an even more hypoallometric  
377 scaling than in figure 3A. Our results therefore suggest that the generalized  
378 hyperallometric reproduction observed in the wild is not the consequence of a  
379 metabolic change in reproductive allocation over life stages. It is rather the result  
380 of differences in environmental history or metabolic capacities between the wild  
381 caught animals used for the scaling. The DEB model is able to incorporate these  
382 differences, and we demonstrate that they can both lead to predicted  
383 hyperallometric reproduction.

384

385 Our analyses investigating different thermal histories or feeding rates show that  
386 they both result in hyperallometry. The associated simulations were obtained  
387 using very simple environmental scenarios, where growth, maturation and  
388 reproduction of *D. labrax* were modeled at constant temperature or feeding rate  
389 varying around 19 °C and 70% of satiety respectively. Future work should  
390 consider more complex environmental histories based on real natural conditions  
391 to see if hyperallometry could still arise. The development of new tracking

392 devices (Brownscombe et al., 2019), biomonitoring tools (Hartman et al., 2015),  
393 or molecular biomarkers of stress or aging (Anastasiadi and Piferrer, 2020;  
394 Sadoul and Geffroy, 2019) will facilitate this goal.

395

396 Our work also shows that variability in some DEB parameters can lead to  
397 apparent hyperallometry when they modify the energy allocation towards  
398 reproduction and growth. Although little information is available on variability  
399 in DEB parameters between individuals of a same species, a change of 10% as  
400 used in our study is below the biological variability previously observed for key  
401 metabolic differences between European sea bass individuals in a controlled  
402 environment (Besson et al., 2019; McKenzie et al., 2014). A recent study  
403 investigated the intraspecies variability in DEB parameters of the copepod,  
404 *Nitocra spinipes*, and found that DEB parameters were following a log-normal  
405 distribution with a standard deviation above 0.15 (Koch and De Schamphelaere,  
406 In press). The 10% of variability in DEB parameters that we tested therefore fall  
407 within this empirical range. While only one parameter was modified at a time in  
408 this study, we can expect individuals to differ from one another for multiple  
409 parameters of the DEB model. However, we show here, using a simplified  
410 scenario, that hyperallometry can also be the consequence of differences in  
411 metabolic capacities between individuals harvested in the wild. Further work is  
412 needed to quantify the genetic basis and heritability of this variability and  
413 therefore the evolutionary potential within a species.

414

415 Similarly to our empirical data, several previous studies have also observed iso-  
416 to hypoallometric reproduction for other aquatic animals, such as brachyuran  
417 crabs (Hines, 1982), isopods (Glazier et al., 2003), or turtles (Iverson et al.,  
418 2019). Out of our three hypotheses, hypoallometry was obtained in old  
419 individuals within the ontogenetic hypothesis or through the variability of some  
420 specific metabolic capacities, such as changes in the allocation fraction to soma  
421 ( $\kappa$ ) or, to a lesser extent,  $[\dot{p}_M]$ . Interestingly, our work suggests that  
422 hypoallometric scaling cannot be obtained through differences in environmental  
423 life history. Consequently, we make the supposition that hypoallometric scaling  
424 found in nature using individuals of various ages necessarily results from

425 variability in intrinsic metabolic capacities probably mostly related to  $\kappa$ . This  
426 parameter has been previously discussed as a potential candidate of  
427 physiological mode of actions of some contaminants (Jager et al., 2010).  
428 Differential exposure to contaminants, or previous toxicological life history, can  
429 explain such variabilities (Ashauer and Jager, 2018; Sadoul et al., 2019).  
430 Variability in  $\kappa$  can probably also be the consequence of genetic differences  
431 within species. Nevertheless, to our knowledge no studies have investigated the  
432 variability in this parameter between genetically different individuals.

433

#### 434 *Concluding remarks*

435 Our study was motivated by recent arguments that current theories of growth  
436 are unable to explain the pattern of hyperallometric reproduction observed in  
437 fish and some other organisms and should therefore be substantially revised  
438 (Marshall and White, 2019; White and Marshall, 2019). Extending the arguments  
439 of Kearney (2019), we have provided simple examples of how hyperallometric  
440 reproduction could plausibly emerge from Dynamic Energy Budget theory  
441 depending on the ontogenetic stage considered within individuals of the same  
442 genotype (i.e. parameter values), the environmental histories experienced  
443 among individuals of the same genotype, and the potential outcome of selection  
444 on individuals with different metabolic genotypes. Our empirical findings based  
445 on laboratory observations of fish reproduction emphasize the limits of making  
446 metabolic generalizations from scaling patterns obtained in nature. This is  
447 mainly because ages and environmental and selection histories of individuals  
448 harvested in the wild are unknown.

449 Taken together, our results highlight the potential biological complexity hidden  
450 behind a simple relationship between weight and reproduction in the wild. We  
451 show that DEB theory is very capable of explaining hyperallometric  
452 reproduction and that it provides a conceptual framework for deciphering the  
453 possible underlying biological mechanisms by which hyperallometric  
454 reproduction manifests in the wild. Our findings show that we have certainly not  
455 'outgrown current growth models' (Marshall and White, 2019). But, interesting  
456 life history observations such as that of hyperallometric reproduction provide  
457 fertile testing ground from which we can hopefully derive more powerful models

458 of population processes in the context of environmental and evolutionary  
459 change.

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#### 462 **DATA AVAILABILITY STATEMENT**

463 The data that support the findings of this study are available as supplementary  
464 material.

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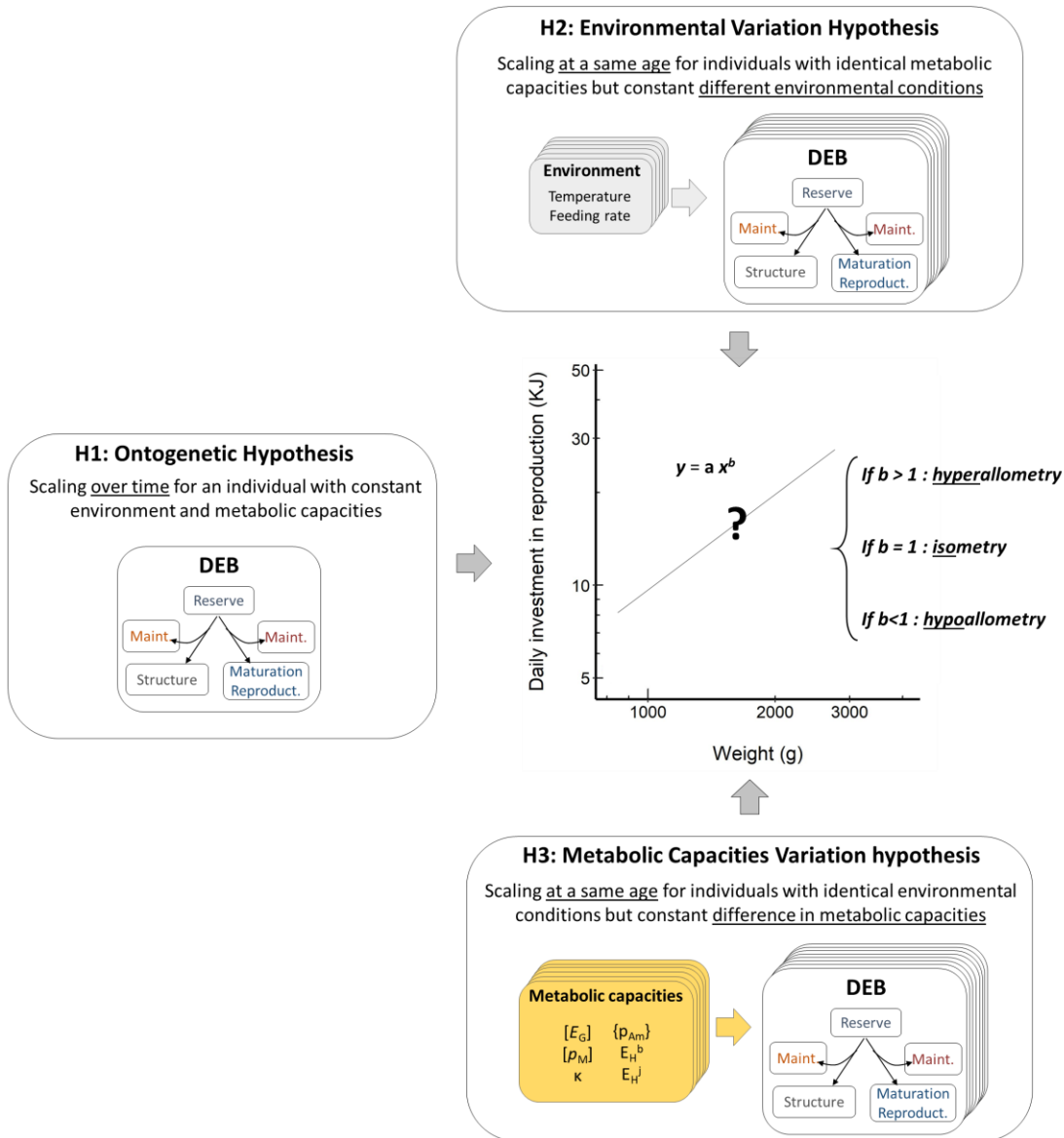
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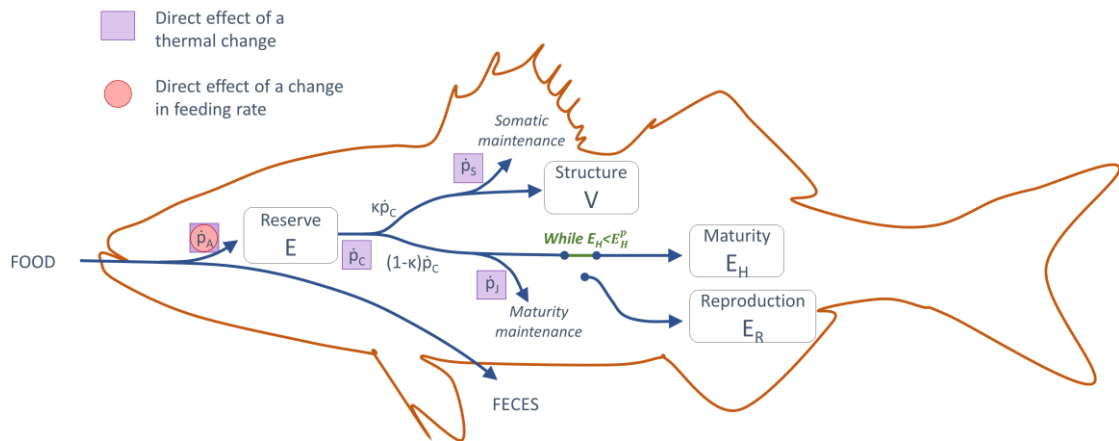
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600  
 601 Figure 1. Three hypotheses testing the emergence of a mass-reproduction scaling  
 602 under the Dynamic Energy Budget (DEB) theory. The DEB theory assumes that  
 603 assimilated energy goes first in a reserve compartment and is then distributed  
 604 between two compartments, the structure or the maturation/reproduction  
 605 (reproduct.), after having paid for their respective maintenance (maint.).  
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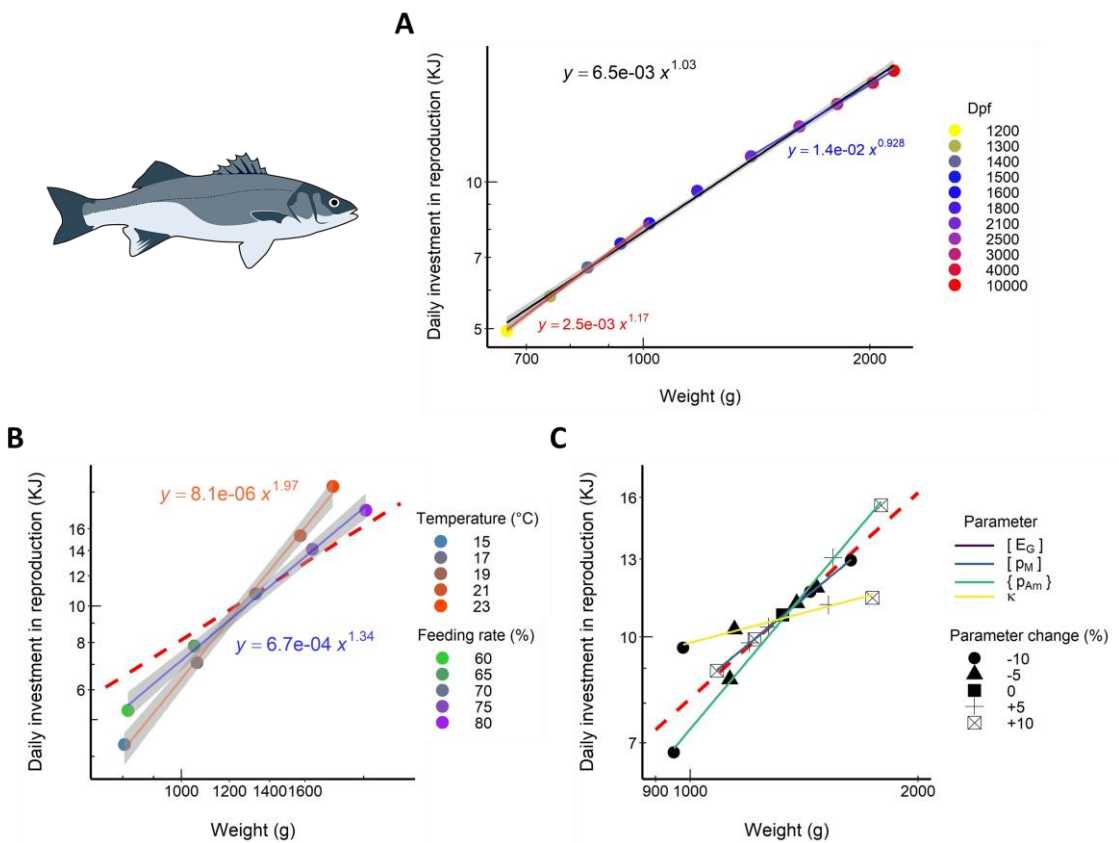


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608 Figure 2. The Dynamic Energy Budget model scheme, indicating the direct effects  
 609 of changing environmental forcing variables (food, temperature) on energy  
 610 allocation in the DEB model.

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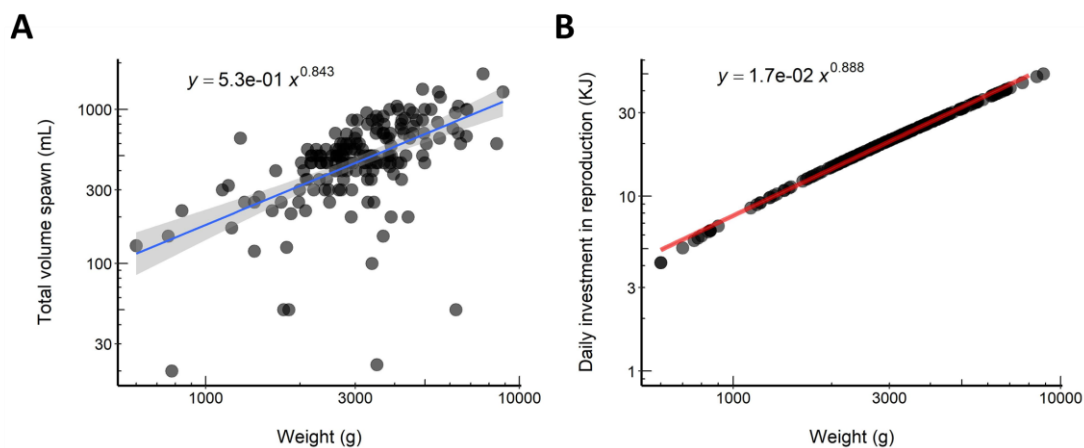
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615 Figure 3. Relationship between reproductive output and mass in *D. labrax* based  
 616 on Dynamic Energy Budget (DEB) simulations. (A) Scaling for a female living at  
 617 19°C and with a feeding rate of 70%. (B) Scaling for females with different

618 thermal or feeding rate life histories. (C) Scaling for females having differences in  
619 their metabolic capacities. For (B) and (C) weights and reproductive outputs  
620 were taken at 2000 days post fertilization (dpf). The isometric scaling is  
621 represented by the dashed red line in (B) and (C). In (A) the isometric line is  
622 equal to the linear model fitting all the points. DEB parameters for *D. labrax* were  
623 used for all simulations. Dpf: Days post fertilization. The two axes are  
624 represented on a log10 scale in all three graphs.

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Figure 4. Reproductive output as function of weight in *D. labrax* reared in laboratory conditions, measured experimentally (A) and simulated by the Dynamic Energy Budget model (B). The two axes are represented on a log scale.