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Title

Multiple working hypotheses for hyperallometric reproduction in fishes under metabolic theory

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Abstract

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

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

INTRODUCTION

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

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

However, a pattern of hyperallometric reproduction observed in wild populations is challenging to interpret when the age, environmental life history and genetic background of the individuals displaying this relationship are unknown (Kearney 2019). This is the case for the data underlying hyperallometric reproduction in fish which derive almost entirely (>98%) from observations of wild individuals (Barneche et al., 2018). Investigating a fecundity to body mass scaling naturally results from the comparison of different sized individuals. But what is driving this variability? Why are large individuals larger? Multiple biological explanations are possible.

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

Second, whether it is the consequence of predation, of sudden environmental challenges or of human activities, selective pressures in the wild are particularly numerous and diversified. These multiple sources of selection are considered as the primary mechanisms of polymorphism in nature (Orr and Smith, 1998). Metabolic capacities driving growth, maturation, reproduction and ultimately fitness are central phenotypic targets of selective pressures (Pettersen et al., 2018). Within a given population, one can expect genetically based variability in metabolic capacities resulting in intrinsic individual differences in assimilation and growth capacity (Besson et al., 2019). Thus, the life history patterns obtained from wild-harvested individuals may also reflect the action of selection.

The environmental and genetic variation inherent in samples from wild populations means that one should be cautious in attributing a pattern of reproductive hyperallometry to metabolic mechanisms involved at the individual level. Rather than using such an empirical observation to dismiss existing models of individual growth and metabolism, one can instead ask under what environmental and genetic circumstances the model would produce the empirical pattern in question. This then leads to clear and testable predictions about what might be occurring in nature. In parallel, detailed laboratory experiments are critical to control and evaluate selective pressures and environmental variabilities and thereby evaluate theoretical expectations.

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

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

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

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

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

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

METHOD

The DEB model for D. labrax

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

The standard DEB model considers the organism to be made up of two macrochemical pools of fixed stoichiometry, the ‘reserve’ E and ‘structure’ (V) which, together with the maturity state E_{H} and the reproduction buffer E_{R}, comprise the state variables of the model as depicted by the 4 compartments in

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

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

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

Simulations based on our 3 hypotheses

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

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

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

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

- The "surface-area-specific maximum assimilation rate" ($\{\dot{p}_{Am}\}$, in J/d/cm^2), driving the maximum amount of energy the animal can assimilate per unit of structural surface when food is *ad libitum*.

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

Testing hypo-, iso- or hyperallometry

Hyperallometry was tested by comparing DEB model outputs for wet weight and daily investment in reproduction on $\log_{10}$ transformed axes. A linear model was fitted to the simulated data and the hypothesis of hyperallometry was accepted if the model slope was higher than one (Figure 1). A scaling with a slope of one is considered isometric while a slope below one is called hypoallometric (Barneche et al., 2018).

Empirical test of reproductive scaling

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

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

RESULTS

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

Ontogenetic Hypothesis

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

Environmental Variation Hypothesis

Within the temperature range investigated here (15 to 23 °C), increasing temperature led to heavier fish at a same age, purely due to the rate effects of temperature on growth (Figure 3B). These fish also invested more in reproduction, and this effect increased disproportionately with body mass. An exponent of almost 2 (1.97) was found for this thermal range. This translates to an investment in reproduction relative to body mass two times (5.33 vs 11.65 J/g wet weight) greater for the biggest fish of the simulation compared to the smallest (806 vs 1778g).

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

Metabolic Capacities Variation Hypothesis

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

Empirical scaling in controlled conditions

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

DISCUSSION

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

Moreover, our empirical data on *D. labrax* obtained in controlled conditions are not consistent with the hyperallometric pattern seen in wild fish. This striking contrast probably derives from the differences between wild and laboratory conditions. Wild caught animals are necessarily more varied in their environmental life histories or intrinsic metabolic capacities than their counterpart laboratory reared animals. Consequently, laboratory conditions permit more powerful tests of ontogenetic scaling relationships because temperature, food availability and water quality can be controlled. In addition, selective pressure is relaxed, reducing the selection based on growth, maturation or reproduction for all animals of the population.

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

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

Our analyses investigating different thermal histories or feeding rates show that they both result in hyperallometry. The associated simulations were obtained using very simple environmental scenarios, where growth, maturation and reproduction of *D. labrax* were modeled at constant temperature or feeding rate varying around 19 °C and 70% of satiety respectively. Future work should consider more complex environmental histories based on real natural conditions to see if hyperallometry could still arise. The development of new tracking devices (Brownscombe et al., 2019), biomonitoring tools (Hartman et al., 2015), or molecular biomarkers of stress or aging (Anastasiadi and Piferrer, 2020; Sadoul and Geffroy, 2019) will facilitate this goal.

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

Similarly to our empirical data, several previous studies have also observed iso- to hypoallometric reproduction for other aquatic animals, such as brachyuran crabs (Hines, 1982), isopods (Glazier et al., 2003), or turtles (Iverson et al., 2019). Out of our three hypotheses, hypoallometry was obtained in old individuals within the ontogenetic hypothesis or through the variability of some specific metabolic capacities, such as changes in the allocation fraction to soma (κ) or, to a lesser extent, $[\dot{p}_M]$. Interestingly, our work suggests that hypoallometric scaling cannot be obtained through differences in environmental life history. Consequently, we make the supposition that hypoallometric scaling found in nature using individuals of various ages necessarily results from variability in intrinsic metabolic capacities probably mostly related to κ. This parameter has been previously discussed as a potential candidate of physiological mode of actions of some contaminants (Jager et al., 2010). Differential exposure to contaminants, or previous toxicological life history, can explain such variabilities (Ashauer and Jager, 2018; Sadoul et al., 2019). Variability in κ can probably also be the consequence of genetic differences within species. Nevertheless, to our knowledge no studies have investigated the variability in this parameter between genetically different individuals.

Concluding remarks

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

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

DATA AVAILABILITY STATEMENT

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

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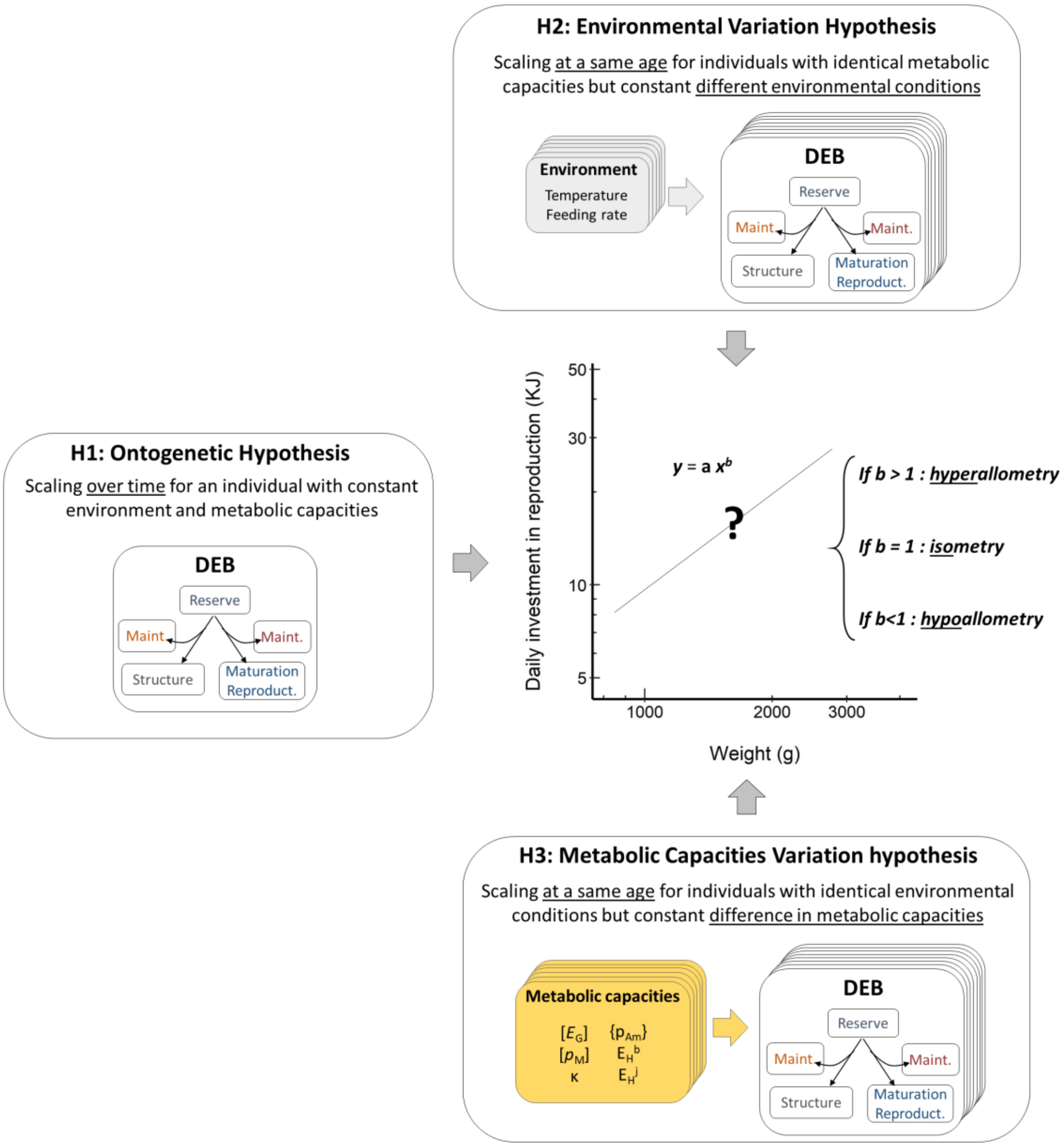

Figure 1. Three hypotheses testing the emergence of a mass-reproduction scaling under the Dynamic Energy Budget (DEB) theory. The DEB theory assumes that assimilated energy goes first in a reserve compartment and is then distributed between two compartments, the structure or the maturation/reproduction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

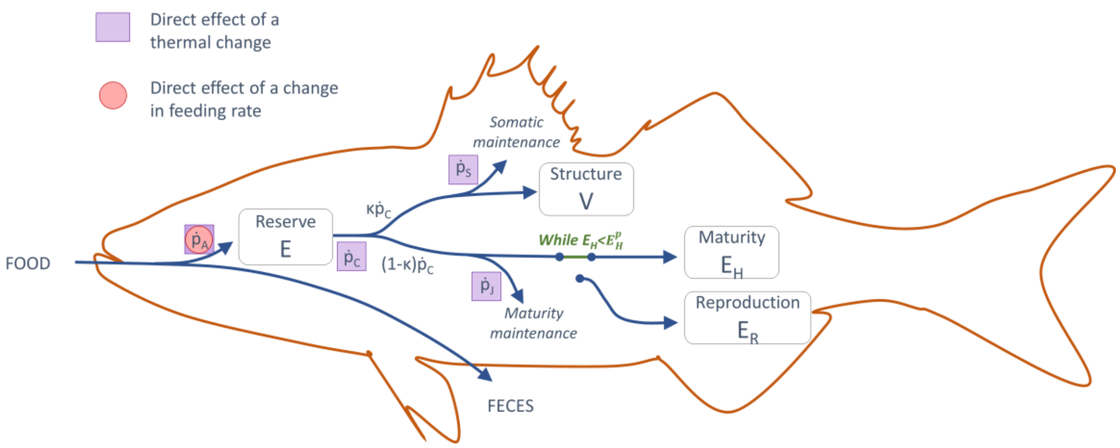

Figure 2. The Dynamic Energy Budget model scheme, indicating the direct effects of changing environmental forcing variables (food, temperature) on energy allocation in the DEB model.

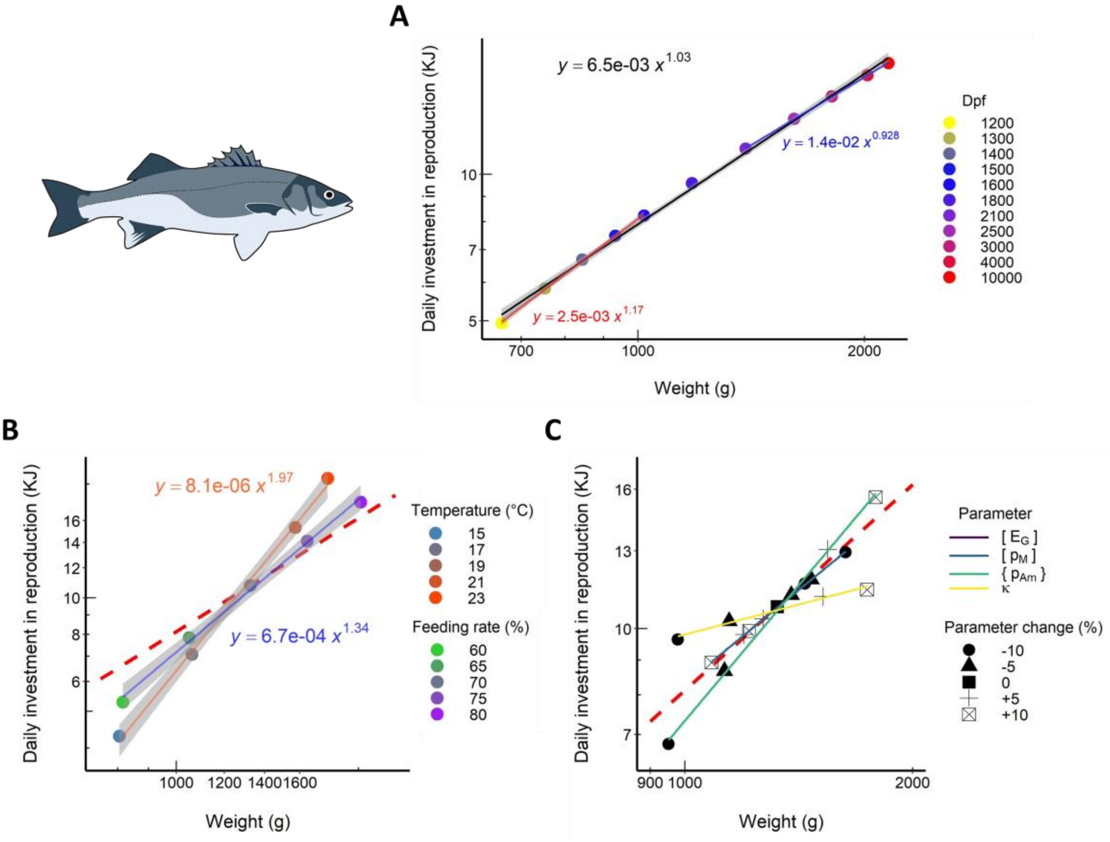

Figure 3. Relationship between reproductive output and mass in *D. labrax* based on Dynamic Energy Budget (DEB) simulations. (A) Scaling for a female living at 19°C and with a feeding rate of 70%. (B) Scaling for females with different

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

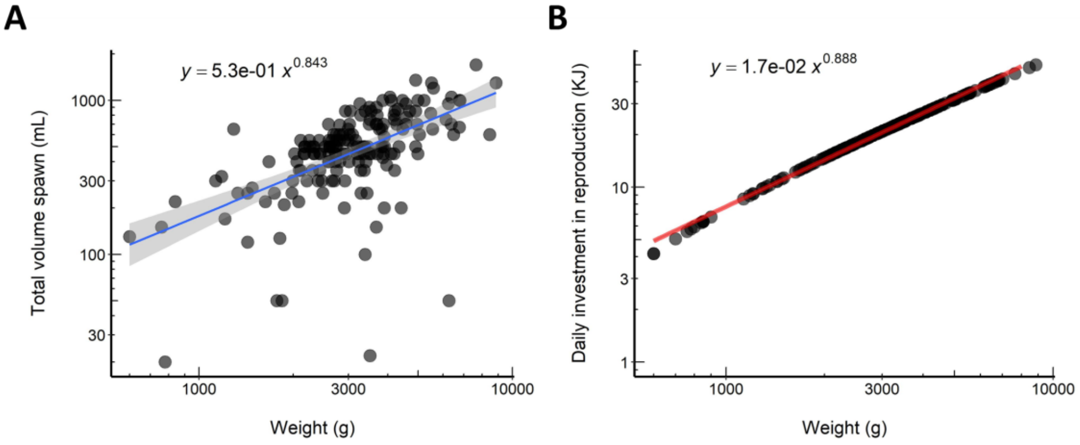

Figure 4. Reproductive output as function of weight in *D. labrax* reared in laboratory conditions, measured experimentally (A) and simulated by the Dynamic Energy Budget model (B). The two axes are represented on a log scale.