
ENERGY INVESTMENT IN GROWTH RATE AND REPRODUCTION

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Abstract

1 With recent results showing that reproduction in fish scales hyperallometrically there is a need to
2 update growth OGMs to reflect this fact. Current OGMs assume optimal intake, an assumption
3 which is not always reflected in the field. This study develops an energy intake focused approach to
4 explaining growth, an area which has not been covered within current literature, and uses the output
5 to determine whether it is intake or maintenance scaling which may be giving rise to disproportional
6 reproductive output in fish.

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1 Introduction

Understanding how organisms grow and what factors play a role in determining growth is not only insightful from the perspective of understanding the world around us, but can also be used to better manage the many fisheries and marine protected areas around the world. An objective which is becoming increasingly important as the oceans' fish stocks continue to be depleted by over fishing. This is compounded by global warming which threatens to alter the structure of the ecosystems even if they are not fished and left in their "natural" state.

Larger fish produce more offspring than smaller ones. In fact, it has been shown that larger fish produce far more offspring than the equivalent mass composed of smaller fish, That is a 2kg fish will produce more offspring than two 1kg fish (Barneche et al., 2018). Larger fish also use energy more efficiently than multiple smaller ones per unit mass. This is due to them having a lower mass specific metabolic rate (Brown, James F. Gillooly, et al., 2004; Kleiber, 1932; Peters, 1983). Additionally, larger mothers produce larger offspring, which are then more likely to survive to adulthood and reproduce (Hixon et al., 2014; C. T. Marshall et al., 2006).

It is already known that metabolic rates is dependant on temperature which in turn will lower fish sizes (Brown, James F. Gillooly, et al., 2004; J. F. Gillooly et al., 2001) and with increasing global temperatures, understanding in greater detail how increased metabolic rates may affect growth is useful in population management.

Key to understanding biological rates and their relationship with mass is the concept of power laws. Many biological traits can be described as scaling to the power of some other biological trait. That is some rate, Y , can be expressed for any mass by $Y = Y_0 m^\beta$, where m is mass (Kleiber, 1932). Power laws can be broadly categorised based on the value of their exponent, β . Where the exponent equals one the relationship is described as isometric or linear, that is the two traits increase at the same rate. Where the exponent does not equal one, the relationship is said to be allometric. That is the trait does not increase at the same rate as the trait being compared against. In cases where the exponent is greater than one, the trait is said to scale super-linearly or hyperallometrically and to scale sub-linearly or hypoallometrically for cases with an exponent of less than one. For the purposes of describing growth these relationships are indispensable.

Traditionally ontogenetic growth models have relied on knowing how large an organism is expected to grow. The von Bertalanffy growth equation relies on knowing the longest a fish can be and the length of the fish at the beginning of measurements (Bertalanffy, 1938; Pütter, 1920). From here, for a known growth rate, the length of the fish after a set amount of time has passed can be predicted.

Another approach has been to try explain growth from an energetic perspective. That is an individuals growth is determined by the amount of energy available to it. Once all costs, such as maintenance, have been paid all remaining energy can be invested towards growth. There are two

frameworks which have been built around this concept; dynamic energy budget (DEB) theory and ontogenetic growth models (OGMs), which will be focused on here.

One of the best known examples of an OGM is the model developed by West et al., 2001. This model is parametrised around the average energy content of animal tissue and asymptotic mass. Asymptotic mass being the mass at which growth has essentially stopped due to metabolic cost and energy intake equalling each other. The model hinges on the scaling with mass between energy intake ($m^{0.75}$, i.e. allometric sub-linear scaling) and maintenance cost (m^1 , i.e. isometric linear scaling). In other words, as mass increases maintenance costs will slowly overtake the intake rate and halt growth.

The framework used by West et al., 2001 was later developed by Charnov, Turner, et al., 2001 to take the cost of reproduction into account and allowing the estimation of lifetime production of offspring. This was done by adding an additional cost which dedicated some portion of mass to reproductive output, essentially gonadosomatic index (GSI). West et al.'s (2001) model was later expanded upon by Hou, Zuo, et al., 2008 to elaborate on the maintenance cost. Hou, Zuo, et al. (2008) takes both the difference between the cost of maintaining tissue and creating it, a factor that is neglected in West et al., 2001, and the cost of digestion into account.

In the above OGMs intake is assumed to scale sub-linearly to the power of 0.75. This is due to the assumption that the individuals are consuming at an optimal rate at all times and therefore the only limitation is their ability to make use of that energy. In this case, intake should theoretically scale to the power of 0.75 (see West et al., 1997). However, this is not always the case in the field. It has been shown that, for non-optimal consumption, steeper scaling can occur (Pawar et al., 2012; Peters, 1983). Additionally, OGMs, like many growth and metabolic models, typically use basal or resting metabolic rate to calculate metabolic cost. This is the minimal metabolic rate of an organism and is typically thought of as the rate of the organism when at relaxed and at rest. However, it has been shown, once factors such as movement are taken into account, that the scaling becomes steeper (Weibel et al., 2004). The issue of non-optimal feeding is addressed somewhat by Hou, Bolt, et al. (2011). However, this growth was only investigated as, essentially, a proportion of optimal consumption and does not address a potential change in scaling of intake rate. Another limitation of the models used in previous OGMs is the dependence on asymptotic mass. The models are entirely dependant on the value of optimal intake and asymptotic mass. All other values, such as metabolic cost, are then derived in relation to these. However, organisms are not born with some inherent restriction to the size they can attain, at least not energetically. If there is surplus energy for a given mass the organism should be able to grow. Relying on asymptotic mass to define the upper bound of attainable mass does not allow for investigation of the mechanisms that underpin asymptotic size in reality.

With two of the key assumptions of current OGMs, that reproduction and metabolism scale isometrically, not holding in the field (Barneche et al., 2018; Pawar et al., 2012; Peters, 1983) there is a need to take an unexplored approach to modelling fish growth, in particular choosing to focus on developing

how intake is described so as to better reflect the real world. To do this an obvious starting point is to model intake as a functional response (Holling, 1959) so as to better reflect real world intake rates in term of consumed biomass over time. Changing the manner in which intake is defined also requires changing metabolic cost, because the two are dependent upon each other in current OGMs. This can be done by defining metabolic rate as a value dependent on current mass rather than asymptotic mass as has been done in OGMs up until this point. This thought process is more mechanistic since an organism has no concept of "How large should I grow?", but rather will acquire as much resources as it capable of at its current life stage and size. Taking this more bottom-up mechanistic approach also allows exploration of what controls how large fish grow to, since as previously mentioned, from an energetic standpoint, an organism can grow indefinitely as long as there is surplus energy available after costs have been paid. Of course, there are also mechanical limitations upon organism size, but once size is constrained to what is known to exist, this should not be an issue. Under the assumption that fish have evolved to maximise reproductive output, using the above framework, simulations can be carried out to demonstrate what conditions need to be met in order to achieve hyperallometric scaling of reproduction from an energetic perspective.

2 Methods

2.1 Redefining OGMs to account for supply

In order to address the issue of supply in the context of an OGM, which can be generically described as $dm/dt = \text{gain} - \text{loss}$, some changes need to be made to the model's terms. The first is to remove the assumption of asymptotic mass and the reliance of cost upon it. Within a traditional OGM the gain term (a) and asymptotic mass are used to define the metabolic cost (b). However, since the assumption of perfect intake is going to be broken, because of the variable supply, this relationship no longer holds. As such, both intake and metabolic cost need to be redefined. Additionally, in light of recent work showing that reproduction scales allometrically and not isometrically, the reproductive cost must also be modified from the form used by Charnov, Turner, et al. (2001) (Barneche et al., 2018; D. J. Marshall and White, 2019)

2.1.1 Redefining Gain

To define intake a natural starting place is the functional response (Holling, 1959). Functional responses are used to define how much an organism consumes for a given resource density and is described by the following equation:

$$f(\cdot) = \frac{aX_r}{1 + ahX_r} \quad (1)$$

where, $f(\cdot)$ is the functional response, a is the search rate, h is handling time and X_r is resource density. For a fixed mass and increasing resource density Eq 1 produces a sigmoidal shape with intake eventually reaching an asymptote after some saturating amount of resources is reached. At lower

resource densities, the intake rate is primarily defined by the search rate with higher search rates yielding higher intake rates. Conversely, at high resource densities, intake rate is approximately equal to the inverse of the handling time (h^{-1}), where lower handling times yield higher intake rates.

An organism's functional response will not remain constant throughout its life history. Search rate and handling time are affected by both the organism's mass and how it interacts with its environment (Pawar et al., 2012). Interactions can be broken into 3D and 2D, that is whether the organism consumes from a 2D "surface" e.g. a cow grazing or a 3D "volume" e.g. a pelagic consumer which consumes prey from within the water column. As such, both handling time and search rate can be defined as Eq. 3 and Eq. 2 respectively.

$$a(m) = a_0 m_t^\gamma \quad (2)$$

$$h(m) = t_{h,0} m_t^\beta \quad (3)$$

A functional response alone is not enough to fully define intake. This is because processing of consumed resources is not one hundred percent efficient which leads to inevitable loss consumed energy. As a result, to achieve the final gain term, a dimensionless efficiency term ϵ is applied. In poikilotherms efficiency is roughly 70% (Peters, 1983)

2.1.2 Redefining Loss

Metabolic cost has previously been dependant upon the gain term within traditional OGMs (see Hou, Zuo, et al., 2008; West et al., 2001). However, for non-maximal intake the relationship will no longer hold true. As a result, this model has taken previously measured values to be used as metabolic cost (see Eq. 4 taken from Peters, 1983 and Table 1 for further details)

$$B_m = 0.14 m_t^\mu \quad (4)$$

Next to take allometric scaling of reproduction into account, the reproductive cost term from Charnov, Turner, et al. (2001) is changed from cm^1 which assumes isometric scaling to cm^ρ . c can be interpreted as the proportion of mass dedicated to reproduction, i.e. the gonadosomatic index (GSI) of the fish (Charnov, Turner, et al., 2001). Just as in Charnov, Turner, et al. (2001) reproductive cost is only taken into account once maturity is reached. Meaning that until a length of time (α) has passed, reproductive cost is considered to be zero.

2.1.3 Full Growth Equation

When all newly defined terms are taken together they produce Eq. 5 and 6 which describe the change in mass for a fish before (Eq. 5) and after maturation (Eq. 6).

$$\frac{dm}{dt} = \epsilon f(\cdot) - B_m \quad m_t < m_\alpha \quad (5)$$

$$\frac{dm}{dt} = \epsilon f(\cdot) - B_m - cm_t^\rho \quad m_t \geq m_\alpha \quad (6)$$

2.2 Estimating Reproductive Output

At any time (t) a reproducing organism devotes some amount of energy to reproduction. This is the product between the amount of mass dedicated to reproduction (cm^ρ) and a declining efficiency term (h_t) which begins at maturity (α) and represents reproductive senescence (Benoît et al., 2018; Stephen C. Stearns, 2000; Vrřilek et al., 2018). In addition to amount of reproduction, the offspring are also subject to mortality (l_t). By combining the two, lifetime reproductive output can be estimated and is described by the "characteristic equation" (Eq. 7) which represents reproductive output in a non-growing population (Arendt, 2011; D. Roff, 1993, 2001; Derek A. Roff, 1984, 1986; Stephen C Stearns, 1992; Tsoukali et al., 2016)

$$R_0 = \int cm_t^\rho h_t l_t dt \quad (7)$$

Mortality is experienced differently by juvenile ($t < \alpha$) and reproducing individuals ($t \geq \alpha$). Mortality of offspring prior to maturity is described as a survival rate $l_t = e^{-Z(t)}$ which is an exponentially decreasing function bounded between zero and one. It controls how many offspring make it to maturity. After maturity, survival is again described as an exponential function which takes time to maturity into account, $l_t = e^{-Z(t-\alpha)}$. Reproductive senescence can be also be estimated as an exponential function which begins after maturity and declines over time ($e^{-k(t-\alpha)}$), where k is the senescence term. When all values are inserted into the characteristic equation, it results in the equation used by Charnov, Turner, et al. (2001) with the inclusion of reproductive senescence (Eq. 8).

$$R_0 = c \int_0^\alpha e^{-Zt} dt \int_\alpha^\infty m_t^\rho e^{-(\kappa+Z)(t-\alpha)} dt \quad (8)$$

In Eq. 8 Z represents instantaneous mortality. This rate has been shown to be related to time of maturation in many taxon groups, and within it follows the relationship $\alpha \cdot Z \approx 2$. This can then be rearranged to estimate instantaneous mortality, $Z \approx 2/\alpha$

2.3 Maximising Reproduction

It is assumed that evolution will converge on metabolic values which maximise fitness. Fitness being defined as how much an individual is able to contribute to the gene pool (Speakman, 2008; Stephen C. Stearns, 2000). To this end, lifetime reproductive output is often used as a measure of fitness (Audzijonyte and Richards, 2018; Brown, Marquet, et al., 1993; Charnov and Berrigan, 1991; Charnov, Turner, et al., 2001; Charnov, Warne, et al., 2007; Speakman, 2008; Stephen C. Stearns, 2000; Tsoukali et al., 2016). Therefore, by maximising for reproductive output, it should become clear what parameters will yield the highest fitness. These parameters will then show whether, within a theoretical framework, hyperallometric scaling arises.

To find all optimal values for reproduction would require Eq. 8 to be analytically solved. However, since no such solution is possible, I simulated the problem numerically to obtain a result. This was done by simulating across values of c and ρ , the parameters of interest between growth (Eq. 5 and 6)

172 and reproductive output (Eq. 8). As c is GSI, it was bound between 0 and 0.5, which encapsulates the
173 values measured within fish (Benoît et al., 2018; Fontoura et al., 2009; D. A. Roff, 1983). To search for
174 any hyperallometry within reproduction, ρ was bound between 0 and 2. The simulation was then run
175 at 0.01 value intervals in both c and ρ over a lifespan of one million days. The results of each simulation
176 were recorded and any non-viable results were discarded. A result was considered non-viable if fish
177 had "shrunk" more than 30% in order to accommodate reproductive costs. Shrinking occurs because
178 the combined loss of energy to metabolism and reproduction is too much for the simulated values at
179 the mass achieved by maturation so the individual experiences a deficit of energy, which is paid by
180 loss in mass until equilibrium is achieved.

181 2.4 answering my questions

182 exponents

183 alpha

184 resources

3 Results

185 3.1 Resources

186 minimum viable resource is dependent upon meta.exp , with 0.75 allowing for less than that of 1 and
187 scaling in between 0.2 for 1 and 0.15 for 0.75. likewise 3D is capable of going lower than 2D due to
188 the higher intake rate. shrinkage plays no role here.

189 3.2 tables and figures

4 Discussion

5 Conclusion

Code and Data Availability

Code is available at: https://github.com/Don-Burns/Masters_Project

Table 1: Table describing parameters used in the model, along with values, units and sources where applicable.

Parameter	Description	Value	Units	Range	Source
m	Mass	-	kg day ⁻¹	-	
B_m	Metabolic Cost	$0.14m^\mu$	kg day ⁻¹	-	Peters, 1983
μ	Metabolic Exponent	-	-	0.75 - 1.0	-
α	Age of maturity	-	day	-	-
c	Reproduction scaling constant	-	kg day ⁻¹	0 - 0.5	-
ρ	Reproduction scaling exponent	-	-	0 - 1.5	-
Z	Rate of instantaneous mortality	$2/\alpha$			Charnov, Turner, et
k	Reproductive senescence	0.01			
ϵ	Resource Conversion Efficiency	0.70	-	-	Peters, 1983
X_r	Resource Density	-	kg	?	-
γ	Search rate scaling exponent	0.68 in 2D 1.05 in 3D	-	-	Pawar et al., 2012
a_0	Search rate scaling constant	$10^{-3.08}$ in 2D $10^{-1.77}$ in 3D	m ² s ⁻¹ kg ^{-0.68} m ² s ⁻¹ kg ^{-1.05}	-	Pawar et al., 2012
β	Handling time scaling exponent	0.75	-	-	Pawar et al., 2012
$t_{h,0}$	Handling time scaling constant	$10^{3.95}$ in 2D $10^{3.04}$ in 3D	kg ^{1-β} s kg ^{1-β} s	-	Pawar et al., 2012

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Reproductive Output (kg)metabolic exponent1

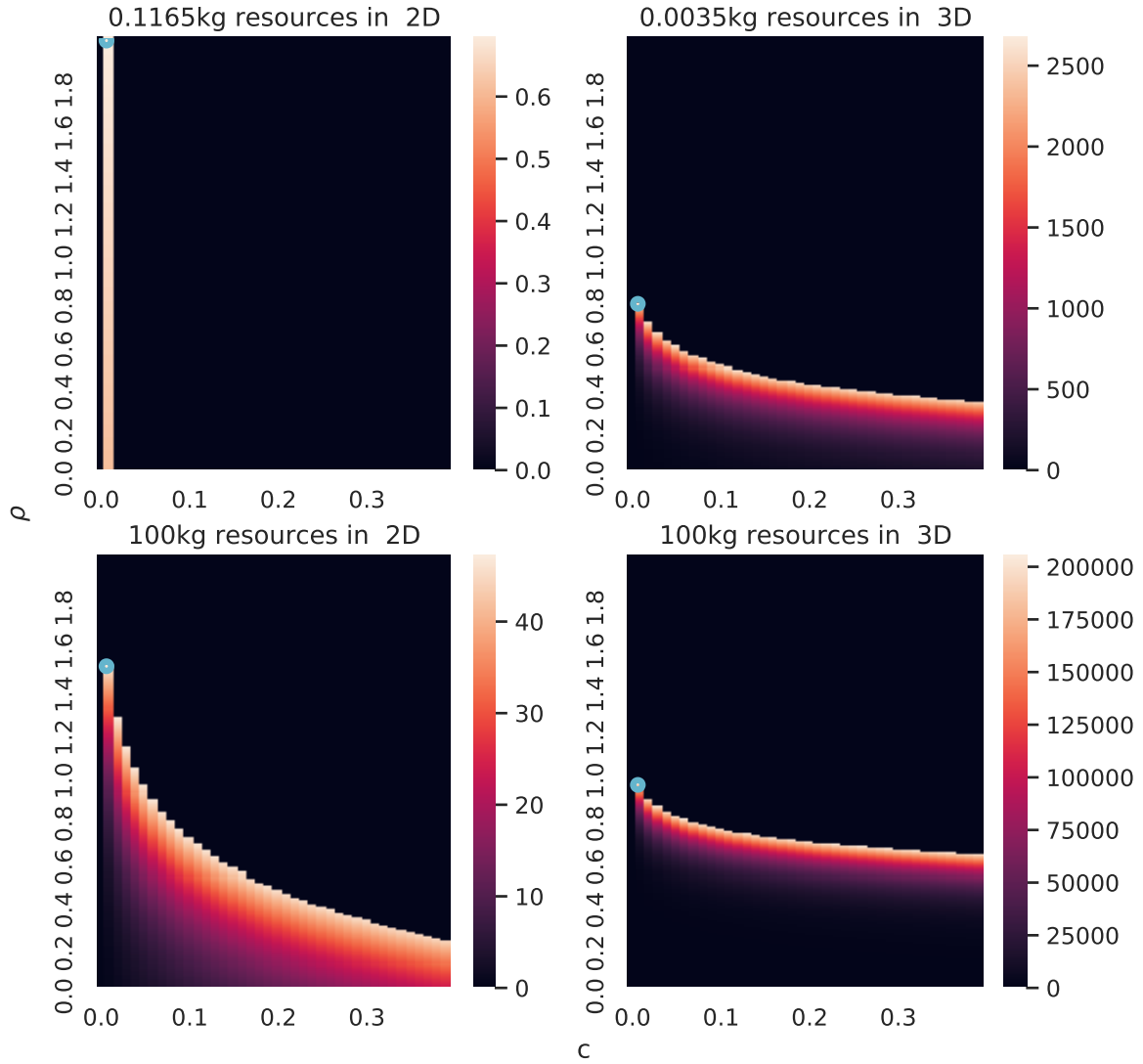


Figure 1: Multiplot with 2D vs 3D and varying resource densities. The optimal value is denoted by the blue circle. The resources used for the low resource scenario (top row) is the minimum amount of resources that allows growth with a c and ρ of 0.01. As would be expected, since has steeper scaling, 3D allows for growth at smaller resource densities than 2D. Low resources in 2D were $\approx 0.1\text{kg}/\text{m}^2$ and $0.00035\text{kg}/\text{m}^2$ in 3D. $100\text{kg}/\text{m}^2$ was used for high resources because, which although unrealistic, ensures that resources are not a limiting factor in the simulations. Hyperallometric scaling is observed in 2D ($\rho = 1.64$ at high resources and 1.99 at low resources (NOTE: This is because 2 is the upper limit of ρ I have simulated here)). Scaling in 3D is slightly hypoallometric $\rho = 0.94$ and $c = 0.01$ at high resources. $\rho = 0.8$ and $c = 0.01$ at low resources The metabolic scaling exponent = 1 in all cases

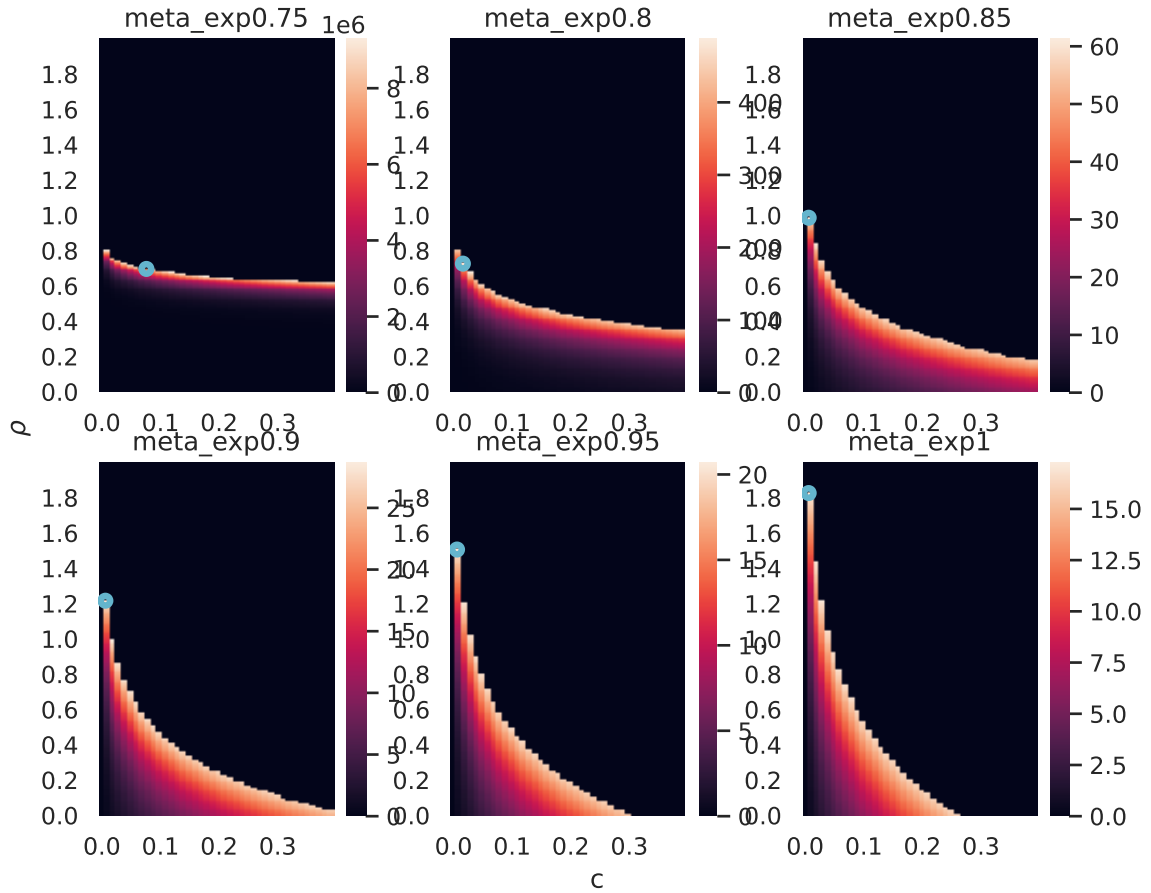


Figure 2: Multiplot with changing metabolic exponents in 2D, ranging from 0.75 to 1, resource density = 0.01, time to maturation is 5 years. It can be seen that higher metabolic responses limit the proportion of mass that can be dedicated to reproduction. However, in exchange, they allow for much steeper scaling. A pattern which is mirrored in 2D and 3D (fig. 3)

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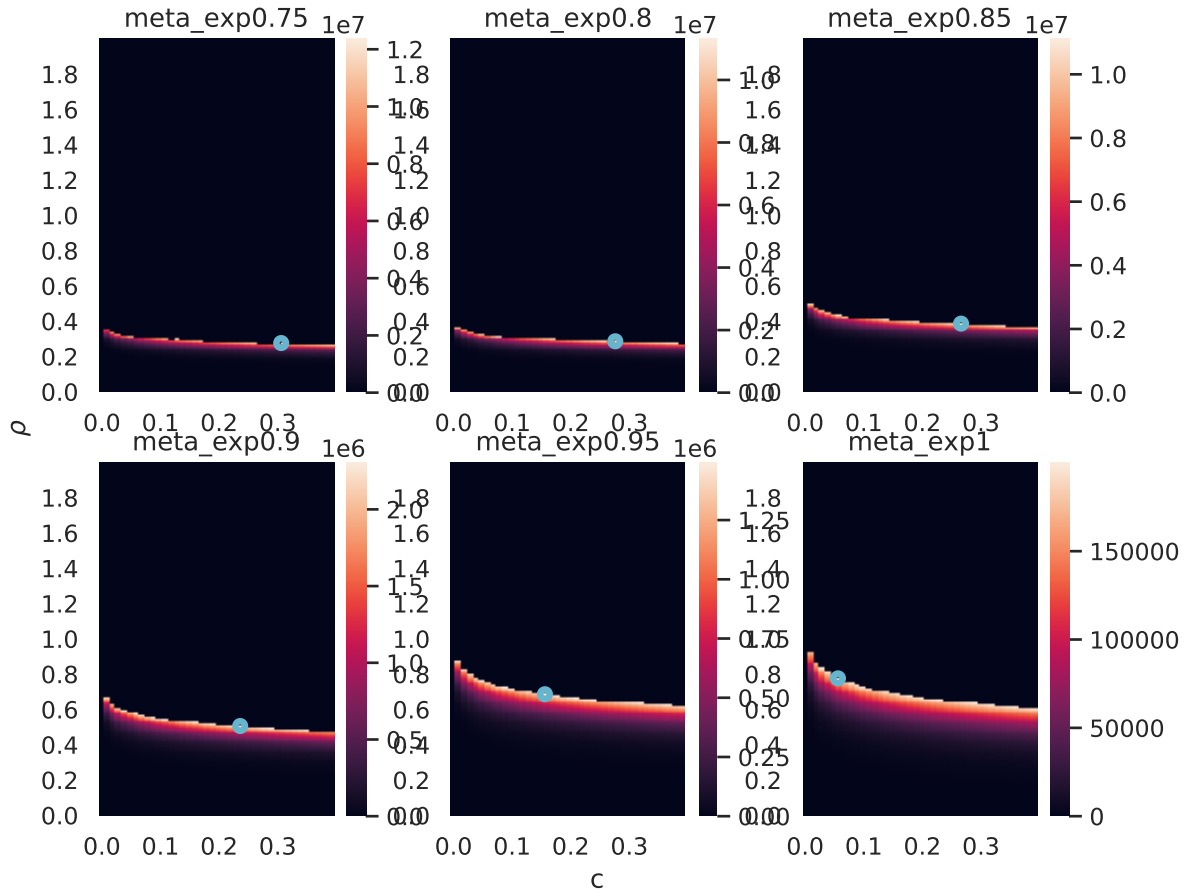


Figure 3: Multiplot with changing exponents in 3D, ranging from 0.75 to 1, resource density = 0.01, alpha is 5 years. See fig 2 for explanation. (NOTE: either 2D or 3D likely belongs in SI)

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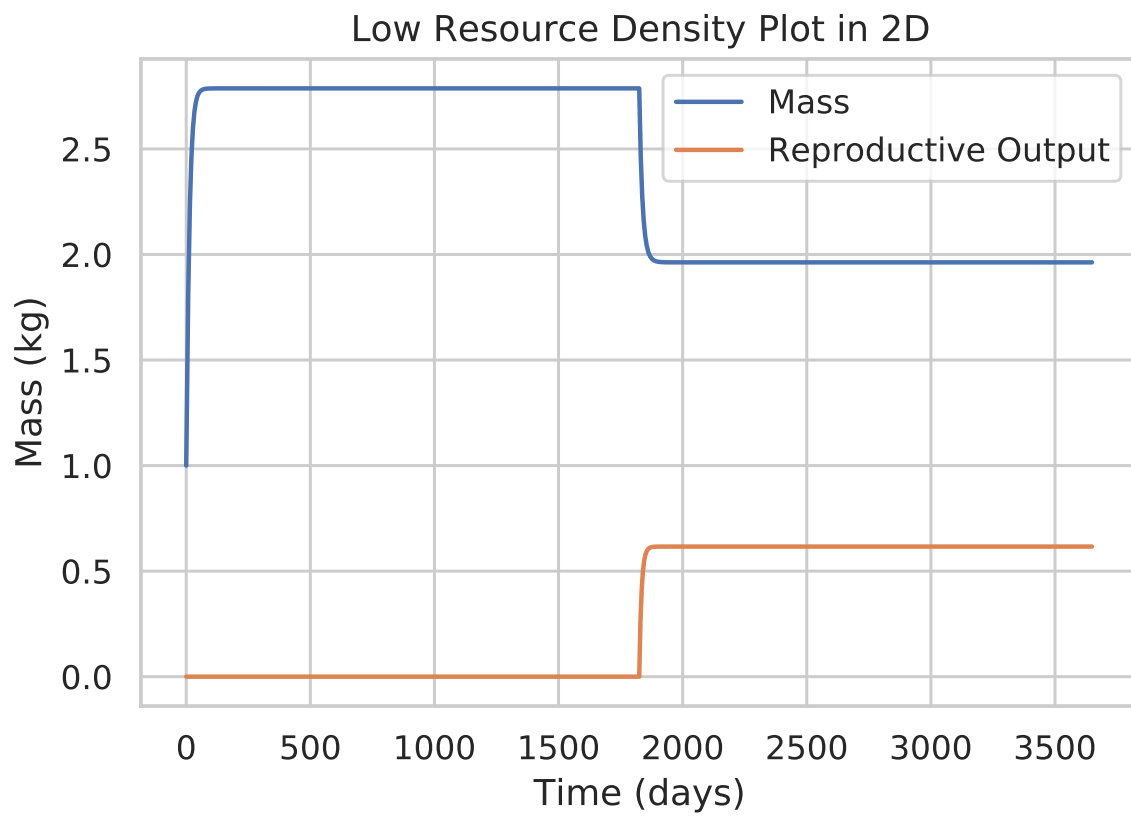


Figure 4: The growth over a fish which consumes in 2D. Maturation occurs at 5 years (1825 days). The fish was allowed to shrink by 30% at the onset of reproduction.

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Supplementary Information

5.1 notes

need section on value conversions and derivations