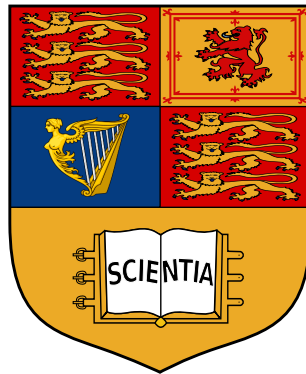# THE ROLE OF RESOURCE SUPPLY IN SHAPING ONTOGENETIC GROWTH AND ALLOCATION IN FISH

## DÓNAL BURNS

*CID: 01749638*

*Imperial College London*

*Email: donal.burns@imperial.ac.uk*

SUBMITTED: AUGUST 27$^{th}$ 2020

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE AT IMPERIAL COLLEGE LONDON

FORMATTED IN THE JOURNAL STYLE OF FUNCTIONAL ECOLOGY

SUBMITTED FOR THE MSC IN COMPUTATIONAL METHODS IN ECOLOGY AND EVOLUTION

# Declaration

I declare this project as my own work. The model presented here was developed in conjunction with my supervisor, Dr. Samraat Pawar, and Ph.D. students Tom Clegg and Olivia Morris. I was responsible for any simulations and data presentation.

**Word Count: 4419**

# Abstract

With recent results showing that reproduction in fish scales hyperallometrically there is a need to update growth OGMs to reflect this fact. Current OGMs assume optimal intake, an assumption which is not always reflected in the field. In this study I develop an energy intake focused approach to explaining growth, an area which has not been covered within current literature, and shows that hyperallometric scaling of reproductive output arises when allowing for variable reproductive scaling and maximising for fitness. The model is applicable to not only fish, but any animals taxon with some simple parameter adjustments. I offer direction for improvements and areas to be developed in order to allow the model to be applicable to any temperature range.

# Acknowledgements

# Contents

# 1  Introduction

Growth is a gateway to understanding how many biological rates change throughout ontogeny. This is because so many biological rates scale with mass (Kleiber, 1932). To date many models have been developed to predict and describe the growth of an organism throughout its lifetime. The three main approaches used are the von Bertalanffy model, the dynamic energy budget (DEB) model and the ontogenetic growth model (OGM), which will be the focus of this study (Bertalanffy, 1938; Kooijman, 1986; Pütter, 1920; West et al., 2001). All of these are energetic based models with varying assumptions, key among which is the scaling of resource supply and metabolic rate with mass. In OGMs supply is thought of as being optimal at all times which leads to the assumption that intake scales to the power of 0.75. Indeed while under optimal conditions this may be true, however, it neglects that this situation is thought to rarely occur in the field (Pawar et al., 2012). This study takes the novel approach of using a mass-specific functional response and assimilation efficiency to describe how intake changes both throughout ontogeny and varying levels of resource availability. While the methodology used here can be used for any animal taxon, in order to investigate growth, a taxon much be chosen to parameterise metabolic rate around. This study will focus on fish.

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 overfishing. 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 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; Marshall et al., 2006).

It is already known that metabolic rate is dependant on temperature which in turn will lower fish sizes (Brown et al., 2004; 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, $\beta$. 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.

One of the best known examples of an OGM is the model developed by West et al., 2001. This model is parameterised 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 (Fig. 5a). 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 latter developed by Charnov et al. (2001) to take the cost of reproduction into account and allowing the estimation of lifetime production of offspring. Hou et al. (2008) latter developed West et al.'s model further by expanding maintenance cost to include the cost of feeding and digestion (specific dynamic action), synthesis of new tissue and activity.

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 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 dependent 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 iso-

6

metrically, 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 terms of consumed biomass over time. Non-optimal supply is a currently unexplored area within growth modelling. This is likely due to the difficulty of directly measuring intake, especially in the field, Perhaps as a result comparatively less is known about consumption. This leads to the need for proxy values to estimate it, for example nutrient flux (Schiettekatte et al., 2020), or drawing broad relationships to approximate consumption, as this study will do. 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 and genetic 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. This study will answer 1) Under what metabolic scaling exponent can hyperallometric reproduction arise, 2)

## 2 Methods

### 2.1 Altering OGMs to account for resource supply

In order to address the issue of supply in the context of an OGM, which can be generically described as $dm/dt = gain - loss$, 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 tradional 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 et al. (2001) (Barneche et al., 2018; Marshall and White, 2019)

7

### 2.1.1 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:

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

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.

$$a(m) = a_0 m_t^\gamma \tag{2}$$

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

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 $\epsilon$ is applied. In poikilotherms assimilation efficiency is roughly 70% (Peters, 1983)

### 2.1.2 Loss

Metabolic cost has previously been dependant upon the gain term within traditional OGMs (see Hou 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).

$$B_m = 0.14 m_t^\mu \tag{4}$$

Next to take allometric scaling of reproduction into account, the reproductive cost term from Charnov et al. (2001) is changed from $cm^1$ which assumes isometric scaling to $cm^\rho$. $c$ can be interpreted as the proportion of mass dedicated to reproduction, i.e. the gonadosomatic index (GSI) of the fish

<sup>147</sup> (Charnov et al., 2001). Just as in Charnov et al. (2001) reproductive cost is only taken into account
<sup>148</sup> once maturity is reached. Meaning that until a length of time ($\alpha$) has passed, reproductive cost is
<sup>149</sup> considered to be zero.

<sup>150</sup> ### 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).

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

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

<sup>151</sup> ## 2.2 Calculating Fitness

<sup>152</sup> At any time ($t$) a reproducing organism devotes some amount of energy to reproduction. This is
<sup>153</sup> the product between the amount of mass dedicated to reproduction ($cm^\rho$) and a declining efficiency
<sup>154</sup> term ($h_t$) which begins at maturity ($\alpha$) and represents reproductive senescence (Benoît et al., 2018;
<sup>155</sup> Stearns, 2000; Vrtílek et al., 2018). In addition to amount of reproduction, the offspring are also
<sup>156</sup> subject to mortality ($l_t$). By combining the two, lifetime reproductive output can be estimated and
<sup>157</sup> is described by the "characteristic equation" (Eq. 7) which represents reproductive output in a non-
<sup>158</sup> growing population (Arendt, 2011; Roff, 1993, 2001; Roff, 1984, 1986; Stearns, 1992; Tsoukali et al.,
<sup>159</sup> 2016)

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

<sup>161</sup> Mortality is experienced differently by juvenile ($t < \alpha$) and reproducing individuals ($t \leq \alpha$). Mortality
<sup>162</sup> of offspring prior to maturity is described as a survival rate $l_t = e^{-Z(t)}$ which is an exponentially
<sup>163</sup> decreasing function bounded between zero and one. It controls how many offspring make it to maturity.
<sup>164</sup> After maturity, survival is again described as an exponential function which takes time to maturity
<sup>165</sup> into account, $l_t = e^{-Z(t-\alpha)}$. Reproductive senescence can be also be estimated as an exponential
<sup>166</sup> function which begins after maturity and declines over time ($e^{-k(t-\alpha)}$), where $k$ is the senescence
<sup>167</sup> term. When all values are inserted into the characteristic equation, it results in the equation used by
<sup>168</sup> Charnov et al. (2001) with the inclusion of reproductive senescence (Eq. 8).

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

<sup>170</sup> In Eq. 8, $Z$ represents instantaneous mortality. This rate has been shown to be related to time of
<sup>171</sup> maturation in many taxon groups, and within it follows the relationship $\alpha \cdot Z \approx 2$. This can then be
<sup>172</sup> rearranged to estimate instantaneous mortality, $Z \approx 2/\alpha$

<sup>173</sup> ### 2.2.1 Maximising Reproduction

<sup>174</sup> It is assumed that evolution will converge on metabolic values which maximise fitness. Fitness being
<sup>175</sup> defined as how much an individual is able to contribute to the gene pool (Speakman, 2008; Stearns,

2000). To this end, lifetime reproductive output is often used as a measure of fitness (Audzijonyte and Richards, 2018; Brown et al., 1993; Charnov and Berrigan, 1991; Charnov et al., 2001, 2007; Speakman, 2008; 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 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 $\rho$, the parameters of interest between growth (Eq. 5 and 6) and reproductive output (Eq. 8). $c$ was bound between 0 and 0.4, which encapsulates the values measured within fish (Benoît et al., 2018; Fontoura et al., 2009; Roff, 1983). Though it has been shown to reach as much as 0.7 in some species (Parker et al., 2018). To search for any hyperallometry within reproduction, $\rho$ was bound between 0 and 2. The simulation was then run at 0.01 value intervals in both $c$ and $\rho$ over a lifespan of one million days. The results of each simulation were recorded and any non-viable results were discarded. A result was considered non-viable if fish had "shrunk" more than 5% in order to accommodate reproductive costs. Shrinking occurs in the model because the combined loss of energy to metabolism and reproduction is too much for the simulated values at the mass achieved by maturation so the individual experiences a deficit of energy, which is paid by loss in mass until equilibrium is achieved. Shrinking is not expected at maturity in reality. Typically, maturity will occur while the organism still has room for growth. It is the onset of reproduction which is considered to slow or stop growth (see Fig. 3). Shrinking can be thought of as starvation in a real organism. If energetic cost are not met then energy reserves in the body, such as fat and muscle, are broken down for energy. It has been shown that some fish are capable of losing up to 10% of their body mass (Berghe, 1992). However, this was during the breeding season and caused by behavioural changes due to parenting. Additionally, individuals were shown to rebound back to their "normal" body mass once the breeding season had ended.

## 2.3 Sensitivity Analysis

In order to determine the roles of metabolic exponent, maturation time and resource density within the model, sensitivity analyses were performed on each parameter with regard to $c$ and $\rho$. This was done by simulating the parameters across multiple values and obtaining the optimal value for $c$ and $\rho$ as described above.

Table 1: Table describing parameters used in the model, along with values, units and sources where applicable. The units of resource density change depending on the dimension of intake. $m^D$ represent either $m^2$ in 2D or $m^3$ in 3D

| Parameter | Description | Value | Units | Range | Source |
|---|---|---|---|---|---|
| $m$ | Mass | - | kg day$^{-1}$ | - | |
| $B_m$ | Metabolic Cost | $0.14m^{\mu}$ | kg day$^{-1}$ | - | Peters, 1983 |
| $\mu$ | Metabolic Exponent | - | - | 0.75 - 1.0 | - |
| $\alpha$ | Age of maturity | - | day | - | - |
| $c$ | Reproduction scaling constant | - | kg day$^{-1}$ | 0 - 0.5 | - |
| $\rho$ | Reproduction scaling exponent | - | - | 0 - 1.5 | - |
| $Z$ | Rate of instantaneous mortality | $2/\alpha$ | | | Charnov et al., 2001 |
| $k$ | Reproductive senescence | 0.01 | | | |
| $\epsilon$ | Assimilation Efficiency | 0.70 | - | - | Peters, 1983 |
| $X_r$ | Resource Density | - | kg/m$^D$ | 0.11 - 30 | - |
| $\gamma$ | Search rate scaling exponent | 0.68 (2D) | - | - | Pawar et al., 2012 |
| | | 1.05 (3D) | | | |
| $a_0$ | Search rate scaling constant | $10^{-3.08}$ (2D) | m$^2$ s$^{-1}$ kg$^{-0.68}$ | - | Pawar et al., 2012 |
| | | $10^{-1.77}$ (3D) | m$^2$ s$^{-1}$ kg$^{-1.05}$ | | |
| $\beta$ | Handling time scaling exponent | 0.75 | - | - | Pawar et al., 2012 |
| $t_{h,0}$ | Handling time scaling constant | $10^{3.95}$ (2D) | kg$^{1-\beta}$ s | - | Pawar et al., 2012 |
| | | $10^{3.04}$ (3D) | kg$^{1-\beta}$ s | | |

# 3 Results

## 3.1 Growth Curve and Maturation Time

As can be seen in Figure 4, growth is very fast within the model. Asymptotic mass is reached by ∼15 days. This makes interpreting any results regarding maturation time difficult because any time after ∼15 days produces the same result (see Fig. S1 - S3). However, as can be seen in Fig. S4, where maturation is occurring early during the growth phase, hyperallotric scaling emerges. This pattern shows in particular at lower resource densities in 3D (Fig. S6 and S5)

## 3.2 Effect of Parameters

### 3.2.1 Resource Density

The scaling relationship emerges as would be expected from the scaling of the functional response. At low resource densities the output of the functional response will scale similarly to search rate. The scaling of which is higher in 3D as resources increase and the response shifts to scaling similarly to the inverse of handling time. At this point $\rho$ starts to take values which are higher in 2D than 3D, because of the higher normalisation constant in 2D.

### 3.2.2 Metabolic Exponent

The expected result is for increasing values of metabolic scaling exponent ($\mu$) for $\rho$ to also increase. This is because the lower values of $\mu$ will result in there being a larger gap between the scaling of intake and maintenance, which allows for steeper scaling in reproduction (see Fig. 5 b) (Marshall and White, 2019). This appears to be the case when analysing $\rho$ with respect to the other parameters where $\mu = 1$ or 0.75 (e.g. Fig. S3 and S4 or Fig. S10 and S12). However, when $\mu$ is explicitly simulated over a variety of values, the trend suggests that increasing $\mu$ allows for higher values of $\rho$.

### 3.2.3 Shrinking

At saturated resource densities, allowing for greater proportions of shrinking enables $\rho$ to be set to larger values in both dimensions. This is perhaps not surprising as increasing the shrinking proportion allows for a larger reproductive cost since all individuals will already be at asymptotic mass at time of maturation.

### 3.2.4 $c$ Values

Estimations of $c$ are low in many cases, especially in 2D. While this may be low compared to the ∼10% - 35% expected (Benoît et al., 2018; Fontoura et al., 2009; Roff, 1983) it is not unprecedented for values of 2% to be observed in some fish (Gunderson, 1997). It may be necessary for the lower bounds of $c$ to be adjusted based on what is expected or even viable in the organisms being simulated.

# 4 Discussion

Some caveats with the results of the model. First, growth is simulated as being extremely fast. As previously stated, asymptotic size was reach by ∼10 days. This is of course not representative of the real world, where individuals generally need several months to years to reach maturity. The rapid growth may be due to several factors. First is that metabolic cost may be underestimated. Similar to West et al. (2001), this study used resting metabolic rate to define metabolic costs. However, this does not take other costs into account such as digestion and locomotion. This was addressed in traditional OGMs by Hou et al. (2008). However, due to the use of asymptotic mass in the parametrisation of this change, the same changes could not be used in this model. Resting metabolic rate and active metabolic rates do not scale in the same way with mass (Gillooly et al., 2001; Weibel et al., 2004). The additional cost of active metabolic rate would cause a steeper scaling within the metabolic cost term, leading to more gradual growth (Fig. 5). As such, inclusion of active metabolic rates, while challenging to measure directly and implement, is needed. Additionally, there may be behavioural or physiological factors that would lead to an altered metabolic rate. In this regard, temperature plays a critical role. It is well documented that a change in temperature will change many biological rates (see Peters (1983), Gillooly et al. (2001) etc.). It has been shown that growth is dependent on temperature within fish. For example, a 1.5°C increase in sea temperatures could result in a 15% decrease in fish lengths (Rijn et al., 2017). The functional response data used in this study is standardised around 15°C (Pawar et al., 2012). Meanwhile the metabolic cost is for an unspecified temperature (Peters, 1983). Using rates where the temperature effect is taken into account is crucial for model accuracy given the variation in rates that occurs over different temperatures. Work such as Barneche et al. (2014) has investigated this effect, however the estimate for metabolic rate is several orders of magnitude lower than what was reported by Peters (1983), which is the rate used in this study. Thus further investigation is required.

In fish metabolic rate has also been shown to drop under starvation (Cook et al., 2000). In homeotherms feeding restriction has also been shown to also lower body temperature, since metabolic rate and core temperature are closely related in homeotherms (Ballor, 1991; Blanc et al., 2003).

Another possible point of error is the estimates for supply. The parameters used from Pawar et al. (2012) are for a spectrum of animals from mammals to insects. It is possible by reanalysing the data for only marine species, or more specifically only within taxon or species, predictions of supply could be improved (Marshall and White, 2019).

A factor that is not taken into account in this model is that resources are not constant over time. This can be implemented within the model by varying resource density over time. The functional response will respond accordingly giving intake which varies through time. One concern with implementing such a response is fluctuations are likely not experienced by all organisms in the same way.

For a fish with a small range a local fluctuation can be measured and described relatively simply. However, for a fish with a very large range there is the possiblity leaving resource poor areas in search of richer waters.

Despite these caveats, the patterns which arise from the model are promising. The qualitative patterns seen in this study should not change even with slower growth. This is because while the exact results are not representative of reality, the relationship between the values is. For example, the manner in which supply and metabolic rate interact for different values of the metabolic scaling exponent. The fact that a higher metabolic scaling exponent will cause intake and metabolic cost to intersect sooner does not change regardless of the absolute values.

In conclusion, the model presented in this study is a promising base which can be expanded upon in a way that was not possible with previous OGMs allowing for much more controlled and detailed explanations of the factors controlling growth. In contrast to all previous work, which assume optimal supply, the concept of varying supply is addressed using functional responses. Additionally, qualitative evidence is provided supporting hyperallometric scaling in fish using energy budget as the basis. The model can easily be applied to any animal taxon, not just fish, with some simple changes. Additionally, there are clear directions to be explored to improve the model's accuracy.

# 5  Conclusion

**Code and Data Availability**

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

# References

Arendt, Jeffrey D. (2011). "Size-fecundity relationships, growth trajectories, and the temperature-size rule for ectotherms". In: *Evolution* 65.1, pp. 43–51. DOI: 10.1111/j.1558-5646.2010.01112.x.

Audzijonyte, Asta and Shane A. Richards (2018). "The energetic cost of reproduction and its effect on optimal life-history strategies". In: *American Naturalist* 192.4, E150–E162. DOI: 10.1086/698655.

Ballor, D. L. (1991). "Effect of dietary restriction and/or exercise on 23-h metabolic rate and body composition in female rats". In: *Journal of Applied Physiology* 71.3, pp. 801–806. DOI: 10.1152/jappl.1991.71.3.801.

Barneche, D. R., M. Kulbicki, S. R. Floeter, A. M. Friedlander, J. Maina, and A. P. Allen (2014). "Scaling metabolism from individuals to reef-fish communities at broad spatial scales". In: *Ecology Letters* 17.9, pp. 1067–1076. DOI: 10.1111/ele.12309.

Barneche, Diego R, D. Ross Robertson, Craig R White, and Dustin J Marshall (May 2018). "Fish reproductive-energy output increases disproportionately with body size". In: *Science* 360.6389, pp. 642–645. DOI: 10.1126/science.aao6868.

Benoît, Hugues P., Douglas P. Swain, Jeffrey A. Hutchings, Derek Knox, Thomas Doniol-Valcroze, and Christina M. Bourne (2018). "Evidence for reproductive senescence in a broadly distributed harvested marine fish". In: *Marine Ecology Progress Series* 592, pp. 207–224. DOI: 10.3354/meps12532.

Berghe, Eric P. van den (1992). "Parental care and the cost of reproduction in a Mediterranean fish". In: *Behavioral Ecology and Sociobiology* 30.6, pp. 373–378. DOI: 10.1007/BF00176171.

Bertalanffy, Ludwig von (1938). "A QUANTITATIVE THEORY OF ORGANIC GROWTH (IN-QUIRIES ON GROWTH LAWS. II)". In: *Human Biology* 10.2, pp. 181–213.

Blanc, Stéphane, Dale Schoeller, Joseph Kemnitz, Richard Weindruch, Ricki Colman, Wendy Newton, Kelly Wink, Scott Baum, and Jon Ramsey (2003). "Energy expenditure of rhesus monkeys subjected to 11 years of dietary restriction". In: *Journal of Clinical Endocrinology and Metabolism* 88.1, pp. 16–23. DOI: 10.1210/jc.2002-020405.

Brown, James H., James F. Gillooly, Andrew P. Allen, Van M. Savage, and Geoffrey B. West (July 2004). "TOWARD A METABOLIC THEORY OF ECOLOGY". In: *Ecology* 85.7, pp. 1771–1789. DOI: 10.1890/03-9000.

Brown, James H., Pablo A. Marquet, and Mark L. Taper (Oct. 1993). "Evolution of Body Size: Consequences of an Energetic Definition of Fitness". In: *The American Naturalist* 142.4, pp. 573–584. DOI: 10.1086/285558.

Charnov, Eric L. and David Berrigan (1991). "Evolution of life history parameters in animals with indeterminate growth, particularly fish". In: *Evolutionary Ecology* 5.1, pp. 63–68. DOI: 10.1007/BF02285246.

Charnov, Eric L., Thomas F. Turner, and Kirk O. Winemiller (2001). "Reproductive constraints and the evolution of life histories with indeterminate growth". In: *Proceedings of the National Academy of Sciences of the United States of America* 98.16, pp. 9460–9464. DOI: 10.1073/pnas.161294498.

Charnov, Eric L., Robin Warne, and Melanie Moses (2007). "Lifetime reproductive effort". In: *American Naturalist* 170.6. DOI: 10.1086/522840.

Cook, J. T., A. M. Sutterlin, and M. A. McNiven (2000). "Effect of food deprivation on oxygen consumption and body composition of growth-enhanced transgenic Atlantic salmon (Salmo salar)". In: *Aquaculture* 188.1-2, pp. 47–63. DOI: 10.1016/S0044-8486(00)00333-1.

Fontoura, Nelson F., Aloísio S. Braun, and Paulo Cesar C. Milani (2009). "Estimating size at first maturity (L50) from Gonadossomatic Index (GSI) data". In: *Neotropical Ichthyology* 7.2, pp. 217–222. DOI: 10.1590/S1679-62252009000200013.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov (2001). "Effects of size and temperature on metabolic rate". In: *Science* 293.5538, pp. 2248–2251. DOI: 10.1126/science.1061967.

Gunderson, Donald R. (1997). "Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes". In: *Canadian Journal of Fisheries and Aquatic Sciences* 54.5, pp. 990–998. DOI: 10.1139/f97-019.

Hixon, Mark a, Darren W Johnson, and Susan M Sogard (Oct. 2014). "BOFFFFs: on the importance of conserving old-growth age structure in fishery populations". In: *ICES Journal of Marine Science* 71.8, pp. 2171–2185. DOI: 10.1093/icesjms/fst200.

Holling, C. S. (1959). "Some Characteristics of Simple Types of Predation and Parasitism". In: *The Canadian Entomologist* 91.7, pp. 385–398. DOI: 10.4039/Ent91385-7.

Hou, Chen, Kendra M. Bolt, and Aviv Bergman (2011). "A general model for ontogenetic growth under food restriction". In: *Proceedings of the Royal Society B: Biological Sciences* 278.1720, pp. 2881–2890. DOI: 10.1098/rspb.2011.0047.

Hou, Chen, Wenyun Zuo, Melanie E. Moses, William H. Woodruff, James H. Brown, and Geoffrey B. West (2008). "Energy uptake and allocation during ontogeny". In: *Science* 322.5902, pp. 736–739. DOI: 10.1126/science.1162302.

Kleiber, Max (1932). "California Agricultural Experiment Station Body Size and Metabolism". In: *Hilgardia Journal of Agricultural Science* 6.11, pp. 315–353.

Kooijman, S. A.L.M. (1986). "Energy budgets can explain body size relations". In: *Journal of Theoretical Biology* 121.3, pp. 269–282. DOI: 10.1016/S0022-5193(86)80107-2.

Marshall, C. Tara, Coby L. Needle, Anders Thorsen, Olav Sigurd Kjesbu, and Nathalia A. Yaragina (2006). "Systematic bias in estimates of reproductive potential of an Atlantic cod (Gadus morhua) stock: Implications for stock-recruit theory and management". In: *Canadian Journal of Fisheries and Aquatic Sciences* 63.5, pp. 980–994. DOI: 10.1139/F05-270.

Marshall, Dustin J. and Craig R. White (2019). "Have We Outgrown the Existing Models of Growth?" In: *Trends in Ecology and Evolution* 34.2, pp. 102–111. DOI: 10.1016/j.tree.2018.10.005.

Parker, Geoff A., Steven A. Ramm, Jussi Lehtonen, and Jonathan M. Henshaw (2018). "The evolution of gonad expenditure and gonadosomatic index (GSI) in male and female broadcast-spawning invertebrates". In: *Biological Reviews* 93.2, pp. 693–753. DOI: 10.1111/brv.12363.

Pawar, Samraat, Anthony I. Dell, and Van M. Savage (June 2012). "Dimensionality of consumer search space drives trophic interaction strengths". In: *Nature* 486.7404, pp. 485–489. DOI: 10.1038/nature11131.

Peters, Robert Henry (Oct. 1983). *The Ecological Implications of Body Size*. Cambridge University Press. DOI: 10.1017/CBO9780511608551.

Pütter, August (Dec. 1920). "Studien über physiologische Ähnlichkeit VI. Wachstumsähnlichkeiten". In: *Pflügers Archiv für die Gesamte Physiologie des Menschen und der Tiere* 180.1, pp. 298–340. DOI: 10.1007/BF01755094.

Rijn, Itai van, Yehezkel Buba, John DeLong, Moshe Kiflawi, and Jonathan Belmaker (2017). "Large but uneven reduction in fish size across species in relation to changing sea temperatures". In: *Global Change Biology* 23.9, pp. 3667–3674. DOI: 10.1111/gcb.13688.

Roff, D. A. (1983). "An allocation model of growth and reproduction in fish." In: *Canadian Journal of Fisheries and Aquatic Sciences* 40.9, pp. 1395–1404. DOI: 10.1139/f83-161.

Roff, Derek (1993). *The Evolution of Life Histories: Theory and Analysis*. Springer Science \& Business Media.

— (2001). "Life History, Evolution of". In: *Encyclopedia of Biodiversity*. Elsevier, pp. 631–641. DOI: 10.1016/B978-0-12-384719-5.00087-3.

Roff, Derek A. (1984). "The evolution of life history parameters in teleosts". In: *Canadian Journal of Fisheries and Aquatic Sciences* 41.6, pp. 989–1000. DOI: 10.1139/f84-114.

— (1986). "Predicting Body Size with Life History Models". In: *BioScience* 36.5, pp. 316–323. DOI: 10.2307/1310236.

Schiettekatte, Nina M.D. et al. (2020). "Nutrient limitation, bioenergetics and stoichiometry: A new model to predict elemental fluxes mediated by fishes". In: *Functional Ecology* November 2019, pp. 1–13. DOI: 10.1111/1365-2435.13618.

Speakman, John R. (2008). "The physiological costs of reproduction in small mammals". In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 363.1490, pp. 375–398. DOI: 10.1098/rstb.2007.2145.

Stearns, Stephen C (1992). *The evolution of life histories*. 575 S81.

— (2000). "Life history evolution: Successes, limitations, and prospects". In: *Naturwissenschaften* 87.11, pp. 476–486. DOI: 10.1007/s001140050763.

Tsoukali, Stavroula, Karin H. Olsson, Andre W. Visser, and Brian R. Mackenzie (2016). "Adult lifetime reproductive value in fish depends on size and fecundity type". In: *Canadian Journal of Fisheries and Aquatic Sciences* 73.9, pp. 1405–1412. DOI: 10.1139/cjfas-2015-0378.

Vrtílek, Milan, Jakub Žák, Radim Blažek, Matej Polačik, Alessandro Cellerino, and Martin Reichard (2018). "Limited scope for reproductive senescence in wild populations of a short-lived fish". In: *Science of Nature* 105.11-12. DOI: 10.1007/s00114-018-1594-5.

Weibel, Ewald R., Leonardo D. Bacigalupe, Beat Schmitt, and Hans Hoppeler (2004). "Allometric scaling of maximal metabolic rate in mammals: Muscle aerobic capacity as determinant factor". In: *Respiratory Physiology and Neurobiology* 140.2, pp. 115–132. DOI: 10.1016/j.resp.2004.01.006.

West, Geoffrey B., James H. Brown, and Brian J. Enquist (1997). "A general model for the origin of allometric scaling laws in biology". In: *Science* 276.5309, pp. 122–126. DOI: 10.1126/science.276.5309.122.

— (2001). "A general model for ontogenetic growth". In: *Nature* 413.6856, pp. 628–631. DOI: 10.1038/35098076.
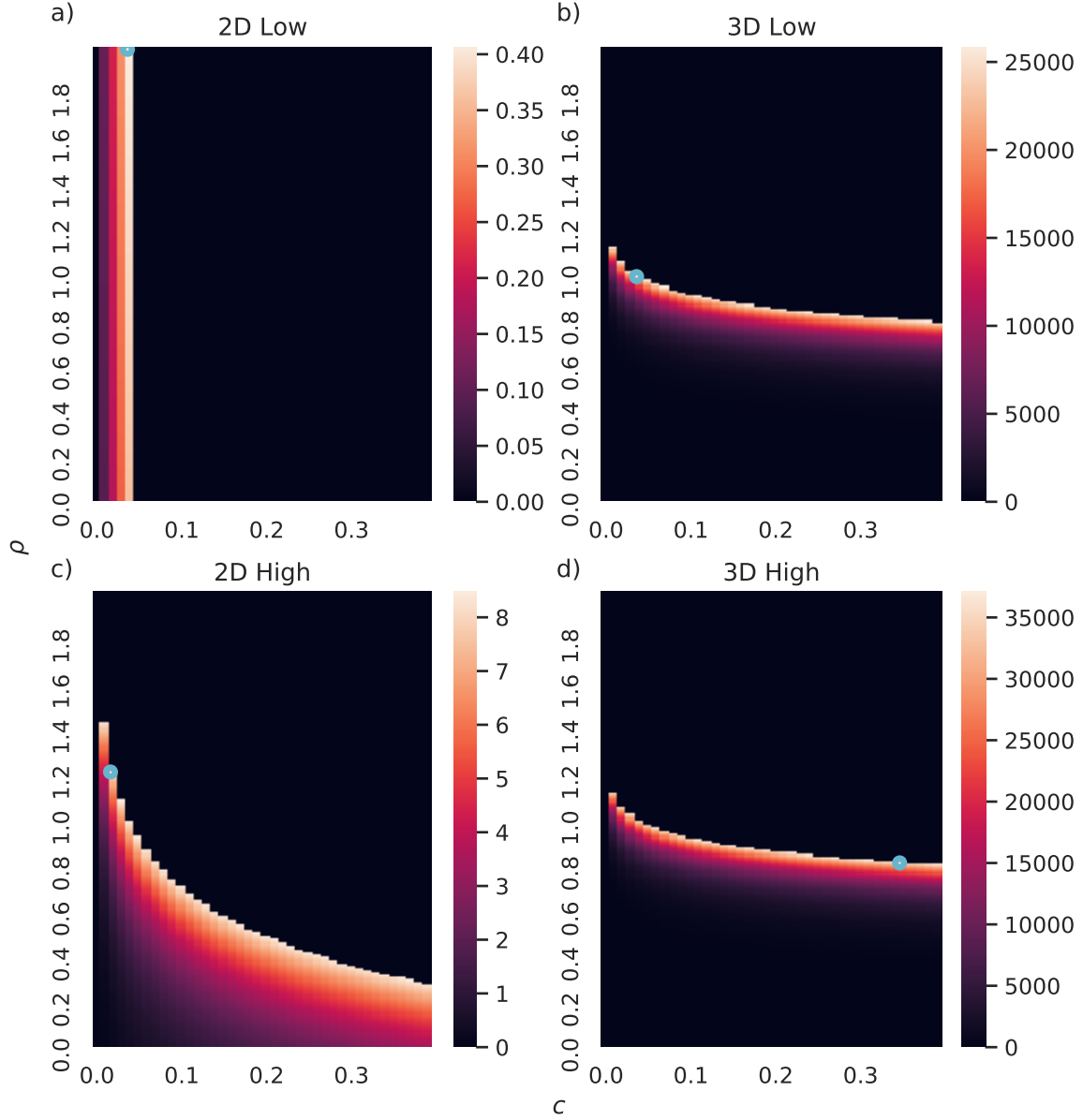
Figure 1: Multiplot with 2D vs 3D and varying resource densities. The optimal value is denoted by the blue circle. The resources used for the low resource scenario (top row) is the minimum amount of resources that allows growth with a $c$ and $\rho$ of 0.01. As would be expected, since has steeper scaling, 3D allows for growth at smaller resource densities than 2D. Low reources in 2D were $\approx 0.1kg/m^2$ and $0.00035kg/m^2$ in 3D. $100kg/m^2$ 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 $\rho$ 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
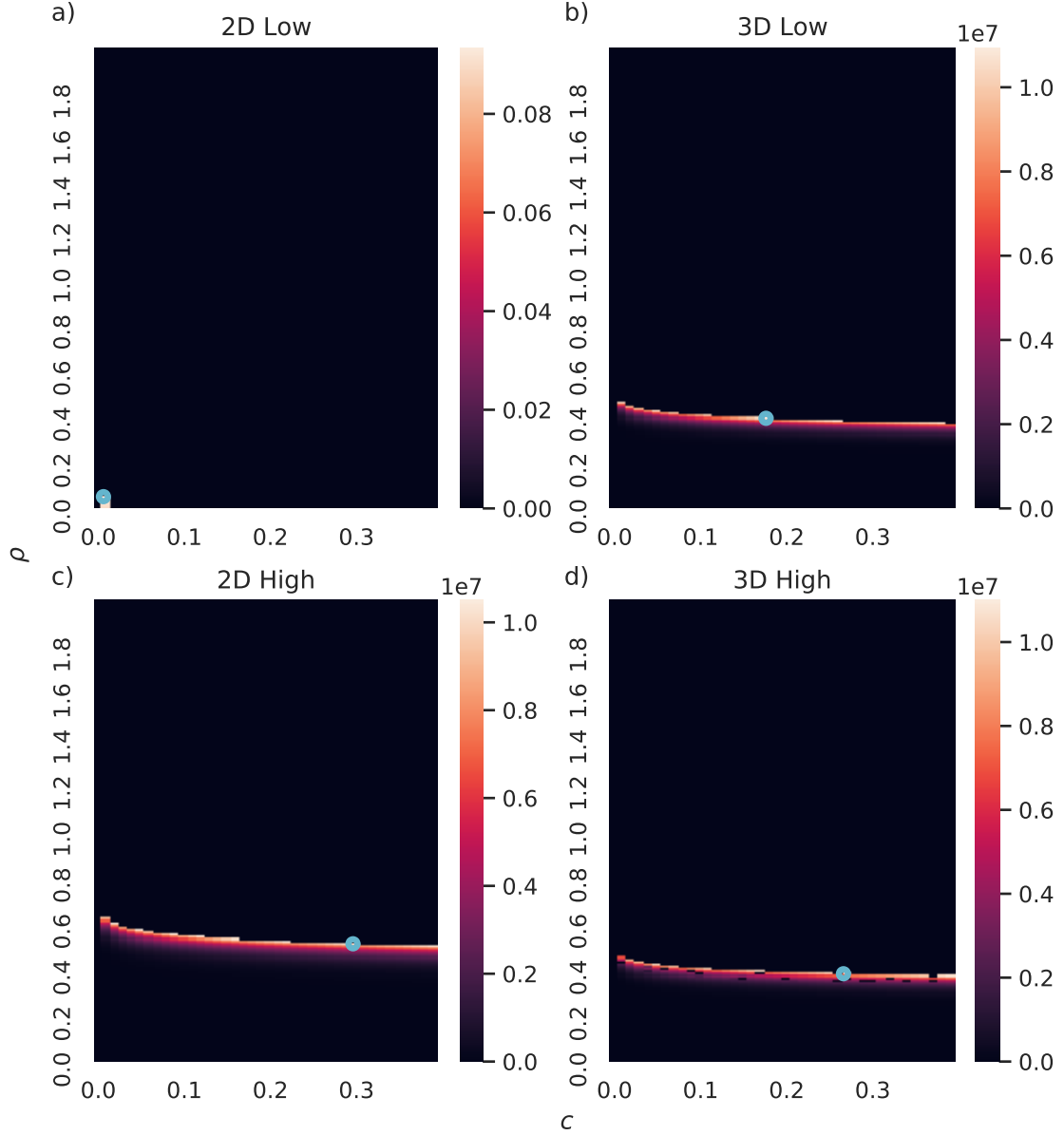
Figure 2: Multiplot with 2D vs 3D and varying resource densities. The optimal value is denoted by the blue circle. The resources used for the low resource scenario (top row) is the minimum amount of resources that allows growth with a $c$ and $\rho$ of 0.01. As would be expected, since has steeper scaling, 3D allows for growth at smaller resource densities than 2D. Low reources in 2D were $\approx 0.1 kg/m^2$ and $0.00035 kg/m^2$ in 3D. $100 kg/m^2$ 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 $\rho$ 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 = 0.75 in all cases
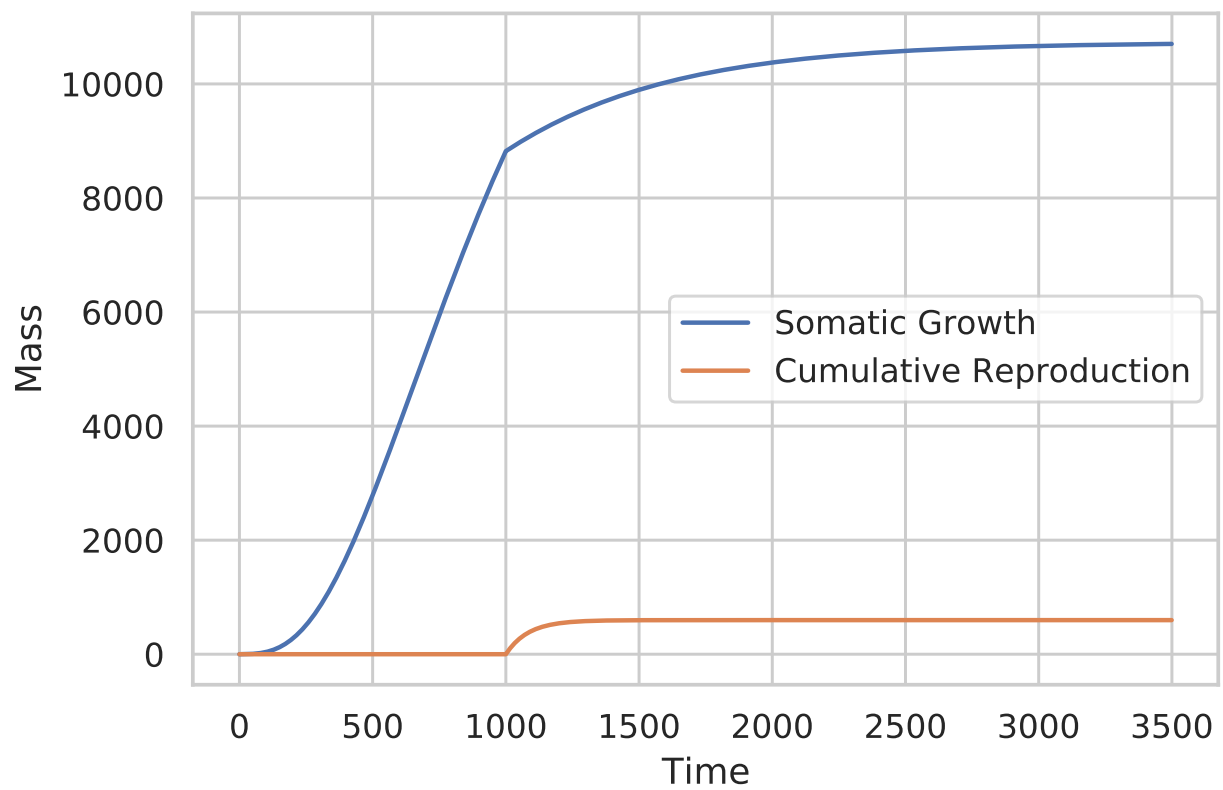
Figure 3: Example of the growth curve and cumulative reproduction expected from a traditional OGM model. Maturation occurs at 1000 days, after which growth is less steep until reaching asymptotic mass.
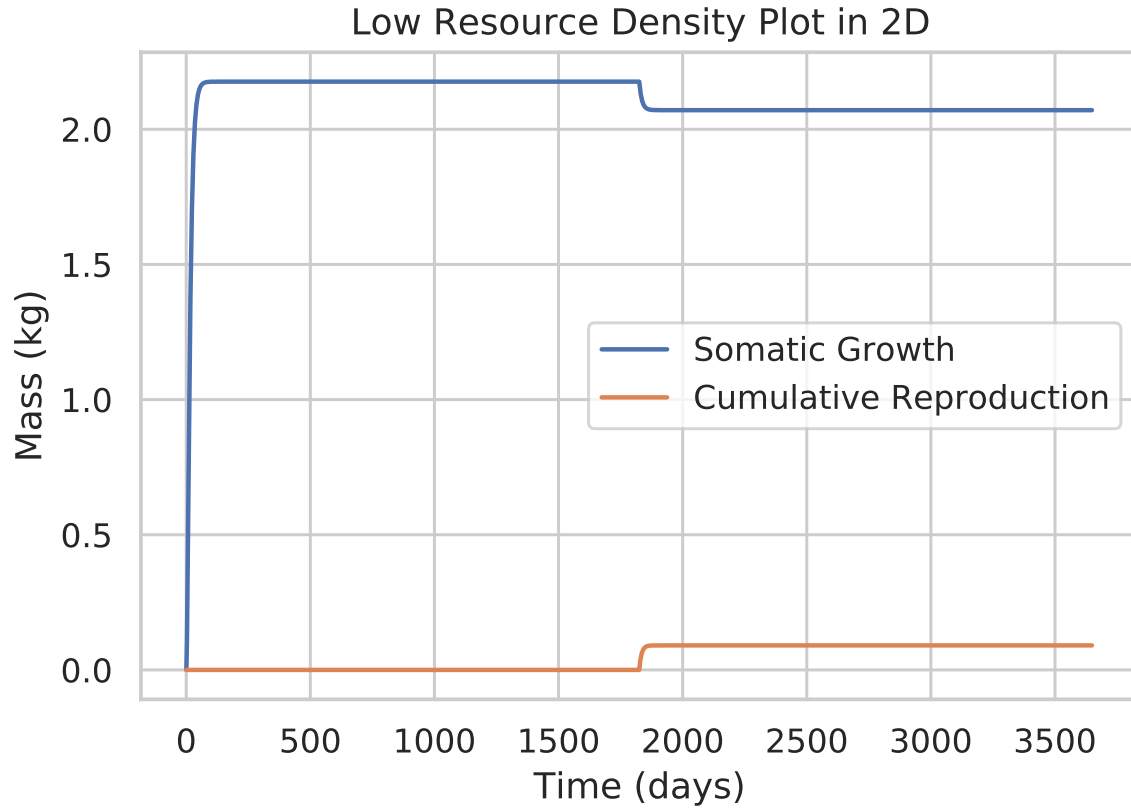
Figure 4: The growth over a fish which consumes in 2D. Maturation occurs at 5 years (1825 days). The fish was allowed to shrink by 5% at the onset of reproduction.
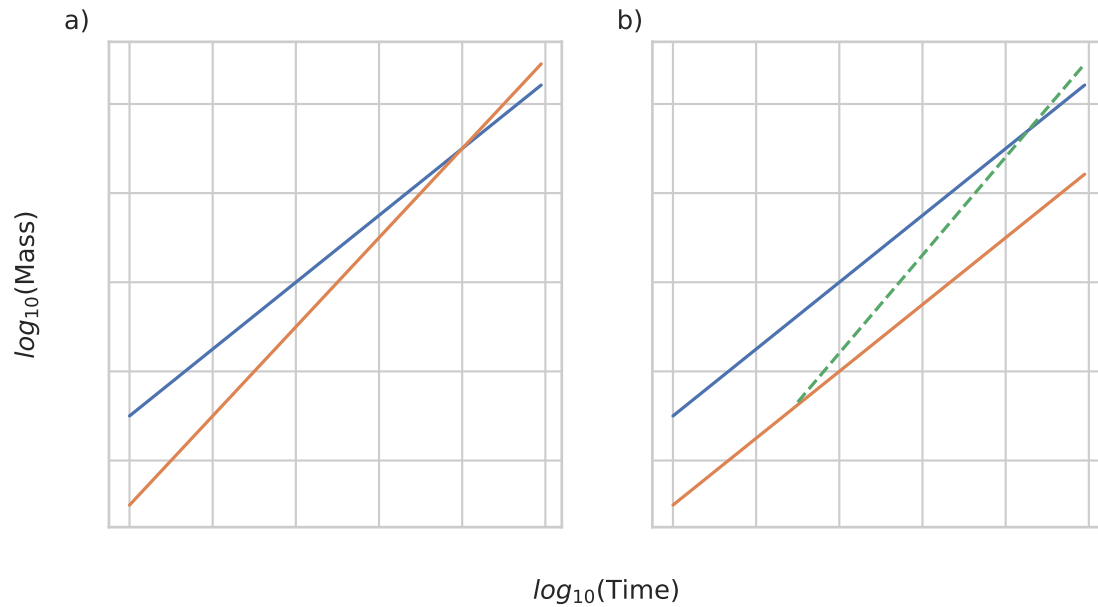


Figure 5: a) shows how maintenance cost outscales supply in a traditional OGM. Growth only stops when maintenance reaches the supply line b) shows scaling for supply and maintenance as equal. Since scaling is equal growth will never stop until the new cost of reproduction is introduced some time during development. Blue line is supply, orange line is maintenance, green dotted line is reproduction

# Supplementary Information

## notes

need section on value conversions and derivations

move any unreferenced sensitivity analyses here.
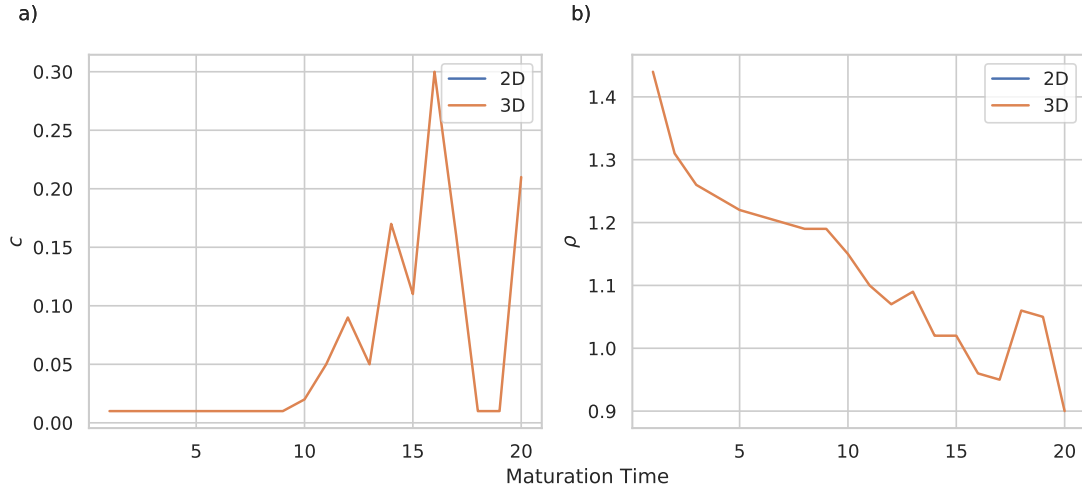
## 5.1 Figures

### 5.1.1 Maturation Time
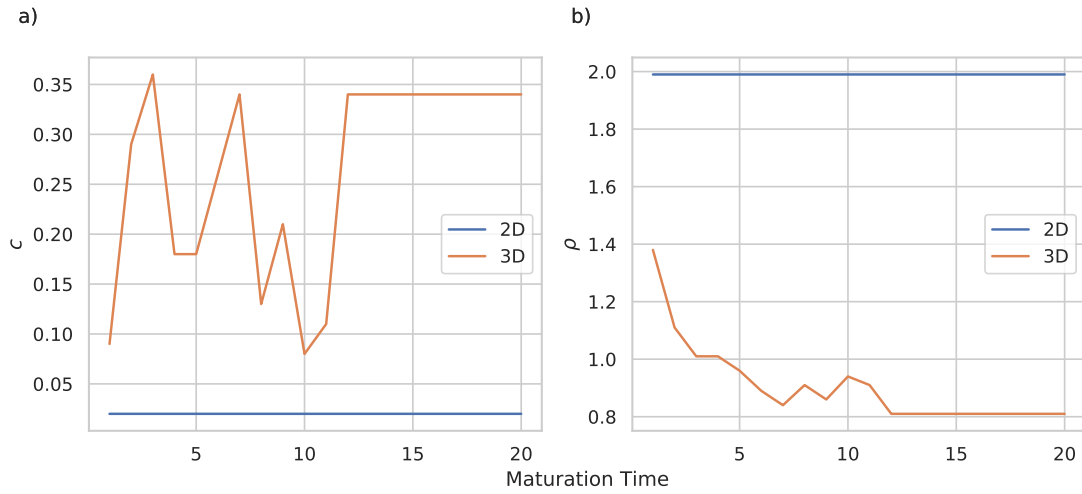


Figure S1: Effect of maturation time on $c$ and $\rho$ where $\mu = 1$ and resource density is low ($0.11$ kg/m$^D$, where $D$ is the dimension).

### 5.1.2 Metabolic Exponent ($\mu$)

### 5.1.3 Resource Density

### 5.1.4 Proportion of Shrinking Allowed
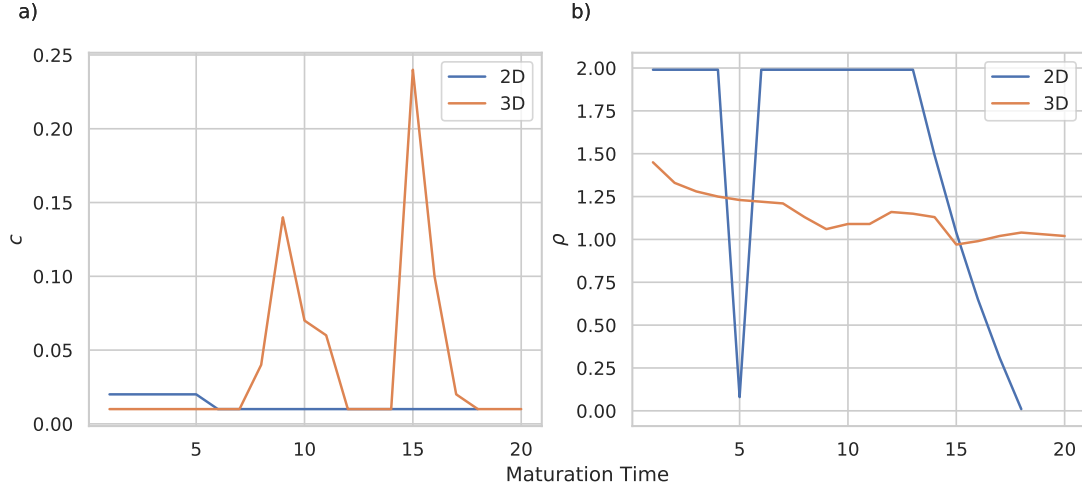
Figure S2: Effect of maturation time on $c$ and $\rho$ where $\mu = 0.75$ and resource density is low(0.11 kg/m$^D$, where $D$ is the dimension).
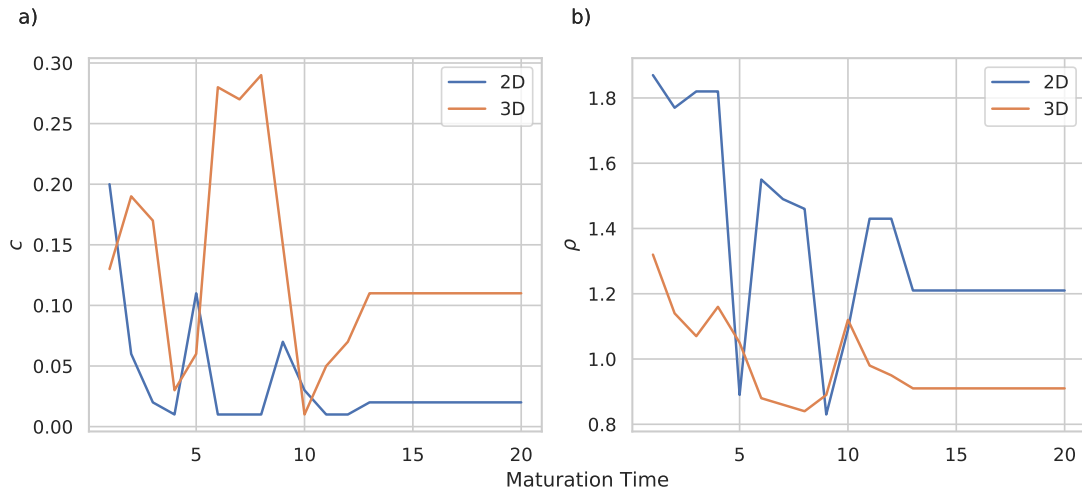


Figure S3: Effect of maturation time on $c$ and $\rho$ where $\mu = 1$ and resource density is high (100 kg/m$^D$, where $D$ is the dimension).
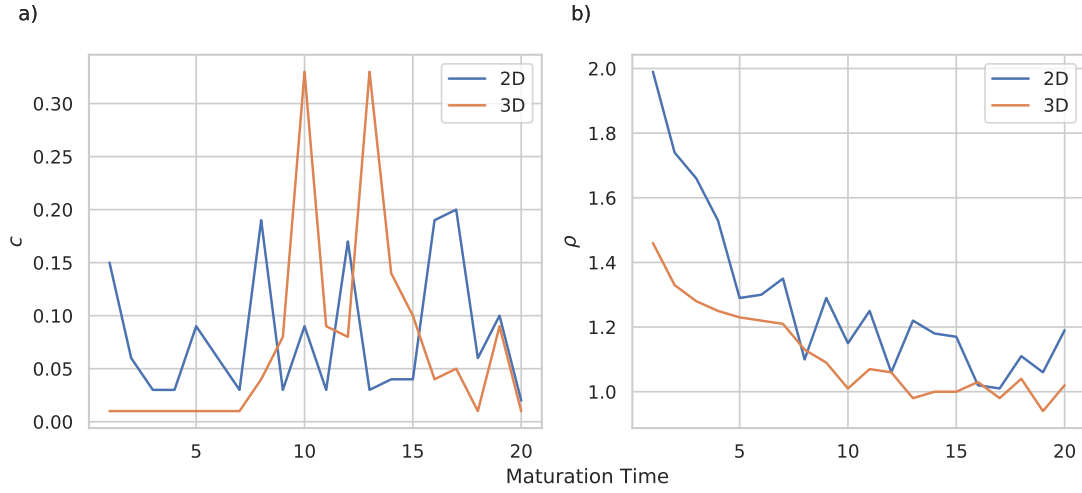
Figure S4: Effect of maturation time on $c$ and $\rho$ where $\mu = 0.75$ and resource density is high (100 kg/m$^D$, where $D$ is the dimension).
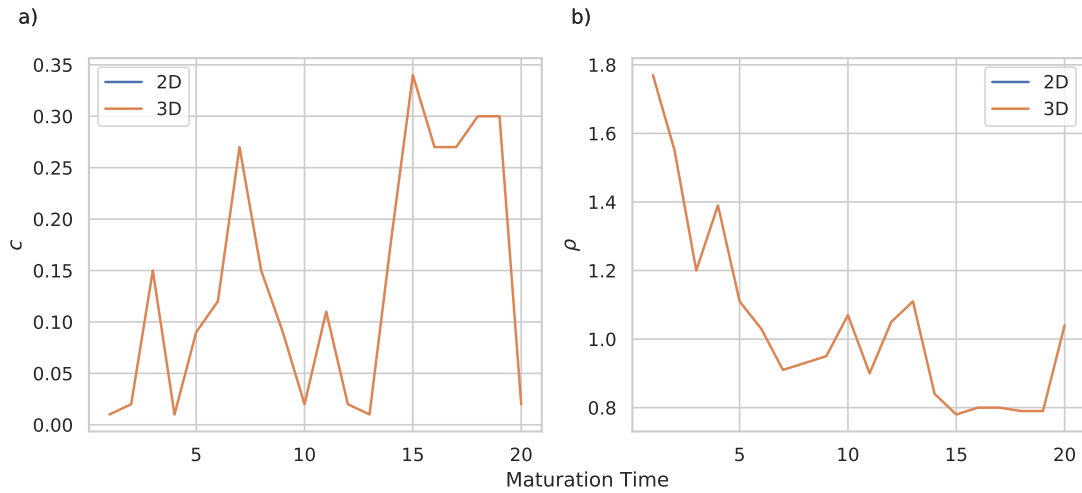


Figure S5: Effect of maturation time on $c$ and $\rho$ where $\mu = 1$ and resource density is very low (0.01 kg/m$^D$, where $D$ is the dimension). At this resource density reproduction can only occur in 3D.

Figure S6: Effect of maturation time on $c$ and $\rho$ where $\mu = 0.75$ and resource density is very low (0.01 kg/m$^D$, where $D$ is the dimension). At this resource density reproduction can only occur in 3D.
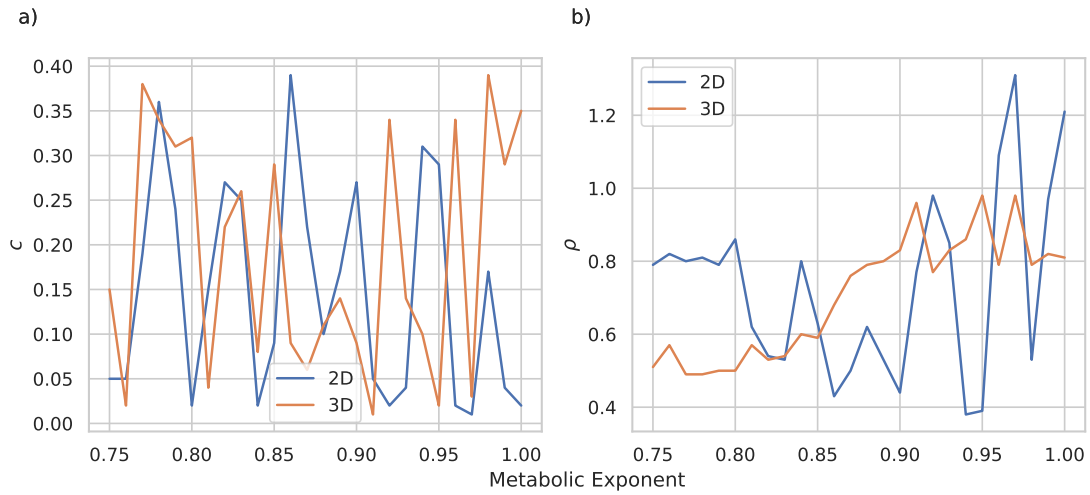


Figure S7: Effect of metabolic on $c$ and $\rho$ where resource density is high (100 kg/m$^D$, where $D$ is the dimension)
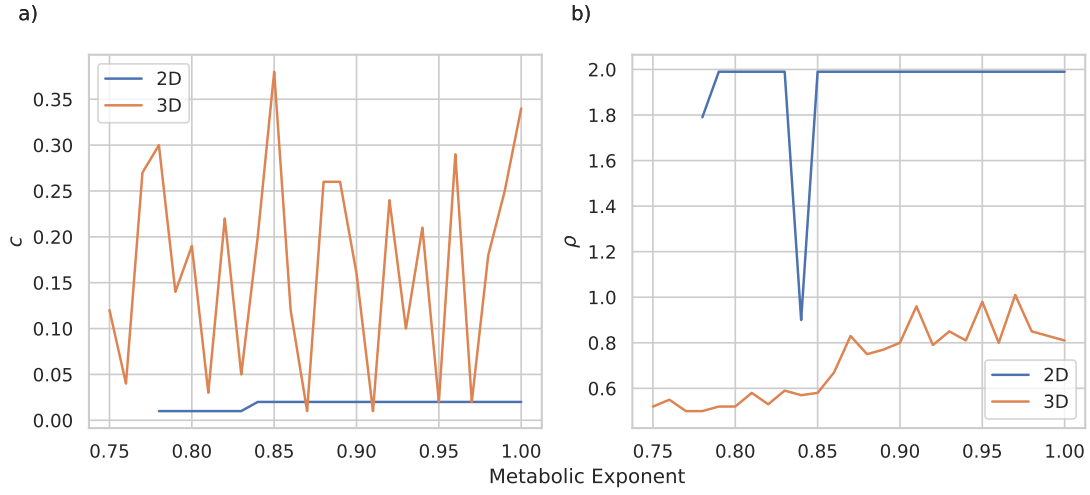
Figure S8: Effect of metabolic on $c$ and $\rho$ where resource density is low (0.11 kg/m$^D$, where $D$ is the dimension)
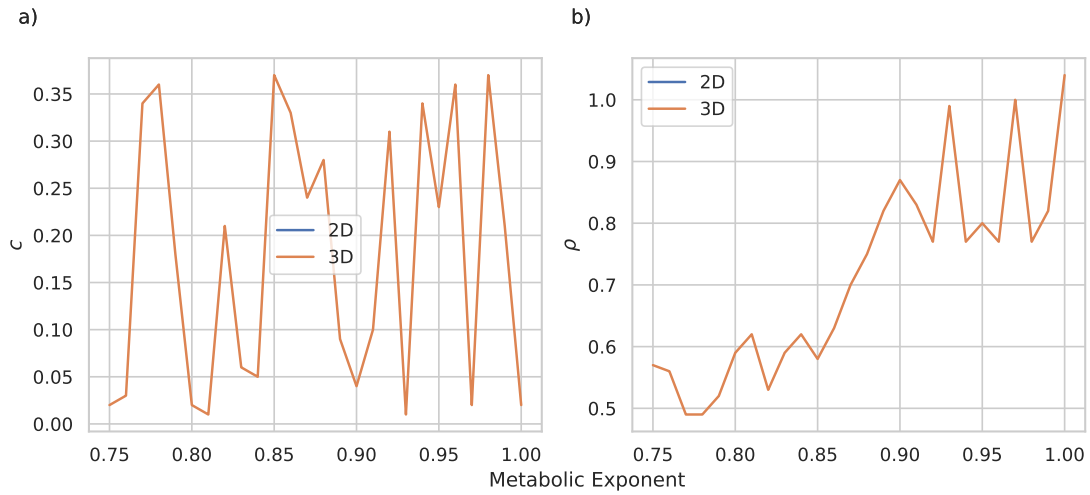


Figure S9: Effect of metabolic on $c$ and $\rho$ where resource density is very low (0.01 kg/m$^D$, where $D$ is the dimension). At this resource density reproduction can only occur in 3D.
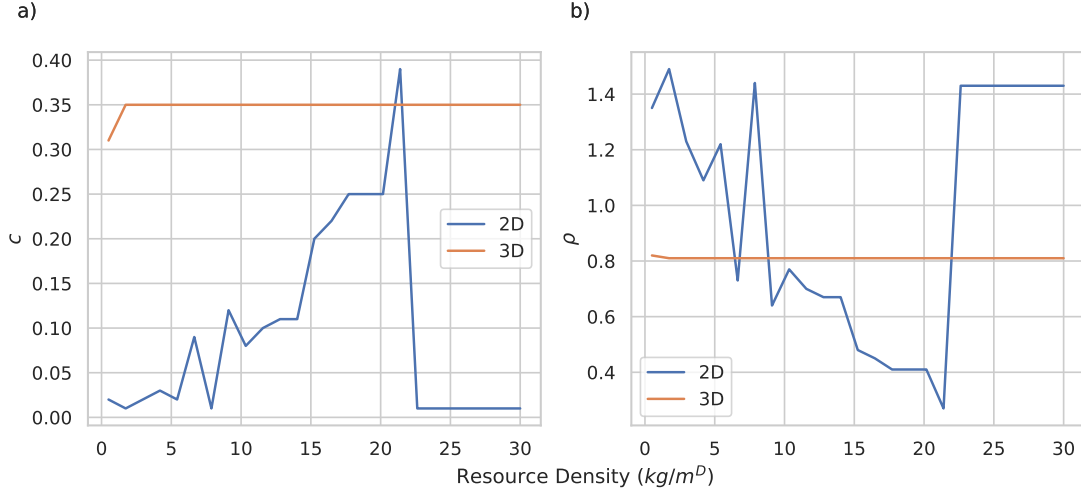
Figure S10: Effect of resource density on $c$ and $\rho$ where $\mu = 1$. Over larger values for resource density. 3D quickly saturates at this density, thus is a nearly straight horizontal line. See Fig. S12 for detail at lower resource density. Units are $kg/m^D$, where $D$ is the dimension.
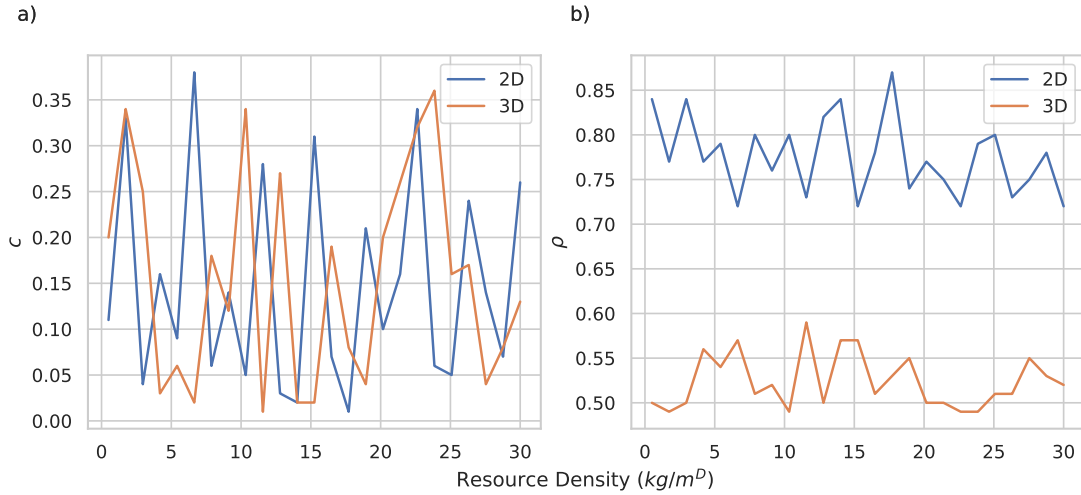


Figure S11: Effect of resource density on $c$ and $\rho$ where $\mu = 0.75$. Over larger values for resource density. There is a lot of numeric instability across resource densities, but the trend appears to be somewhat stable around ∼0.8 in 2D and ∼0.53 in 3D See Fig. S12 for detail at lower resource density. Units are $kg/m^D$, where $D$ is the dimension.
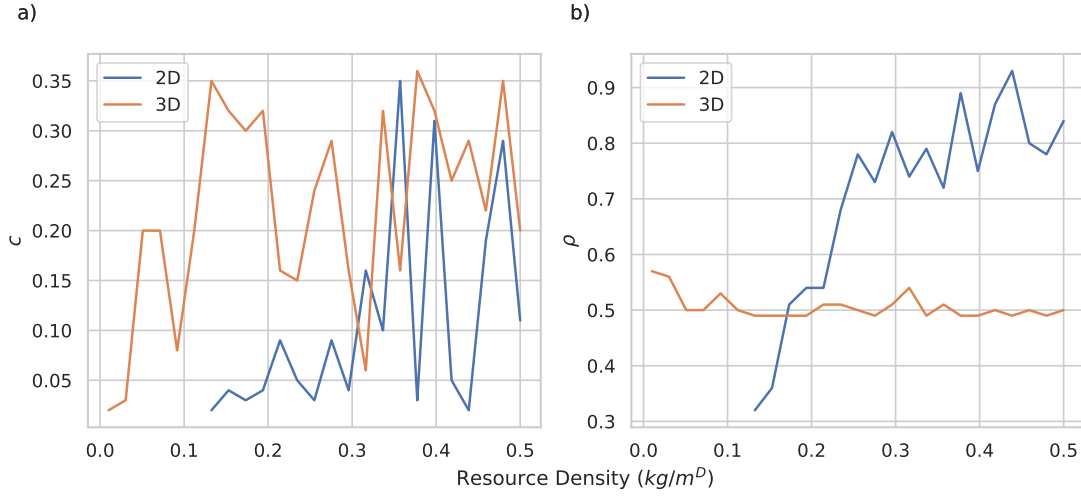
Figure S12: Effect of resource density on $c$ and $\rho$ where $\mu = 0.75$. Demonstrates the expected trend that under limiting resources the higher scaling of 3D search rate allows for steeper reproductive scaling (Table 1). As resources increase and supply shifts more towards being defined by the inverse of handling time, steeper scaling in 2D allows for higher $\rho$ values. Units are $kg/m^D$, where $D$ is the dimension.
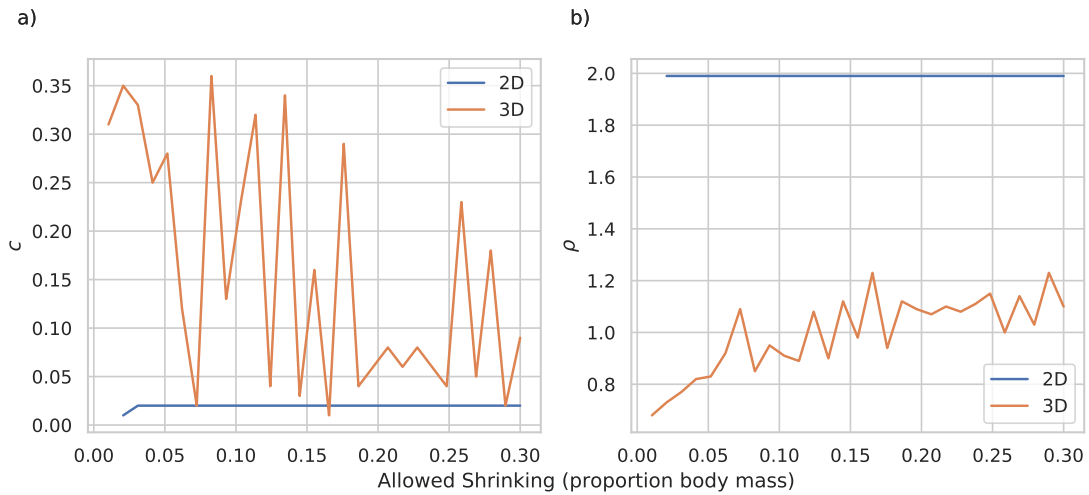


Figure S13: Effect of proportion of shrinking allowed on $c$ and $\rho$ where $\mu = 1$ and resource density is low (0.11 kg/m$^D$, where $D$ is the dimension)
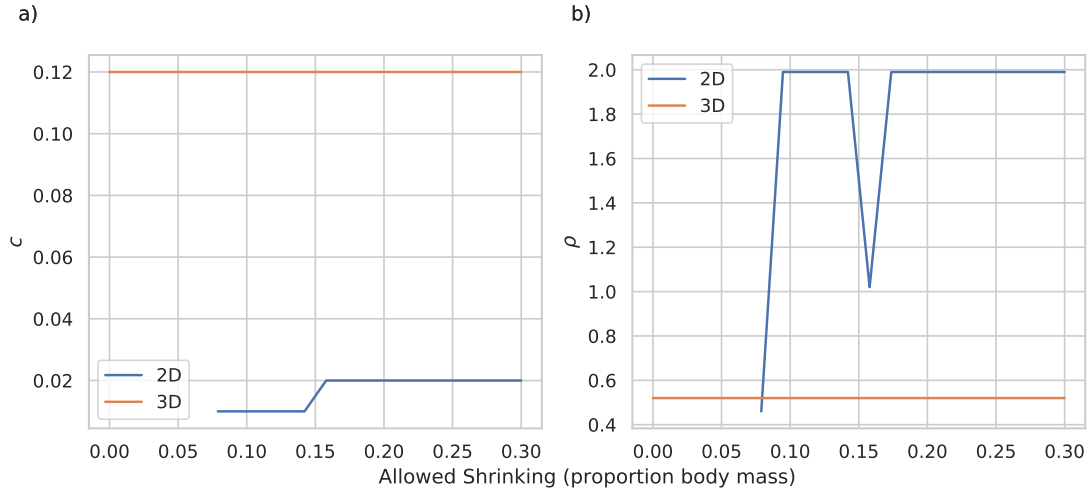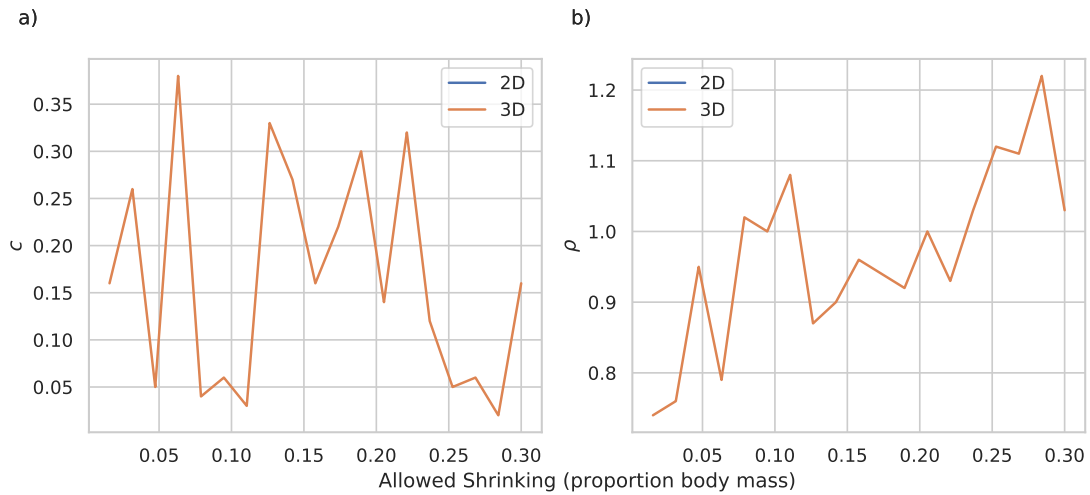
Figure S14: Effect of proportion of shrinking allowed on $c$ and $\rho$ where $\mu = 0.75$ and resource density is low ($0.11$ kg/m$^D$, where $D$ is the dimension)



Figure S15: Effect of proportion of shrinking allowed on $c$ and $\rho$ where $\mu = 1$ and resource density is very low ($0.01$ kg/m$^D$, where $D$ is the dimension). The resource density only allows for reproduction to occur on 3D.
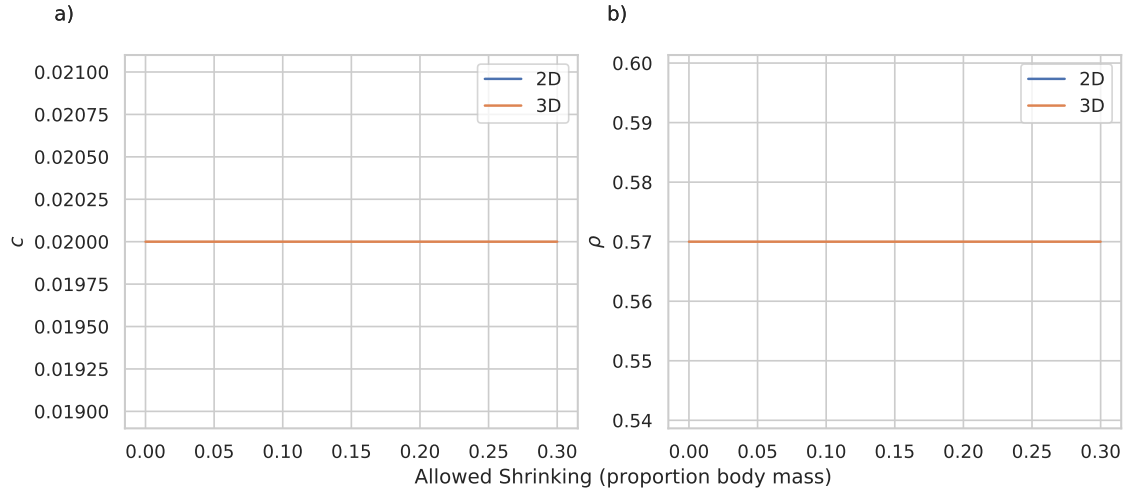
30

Figure S16: Effect of proportion of shrinking allowed on $c$ and $\rho$ where $\mu = 0.75$ and resource density is very low (0.01 kg/m$^D$, where $D$ is the dimension). The resource density only allows for reproduction to occur on 3D.
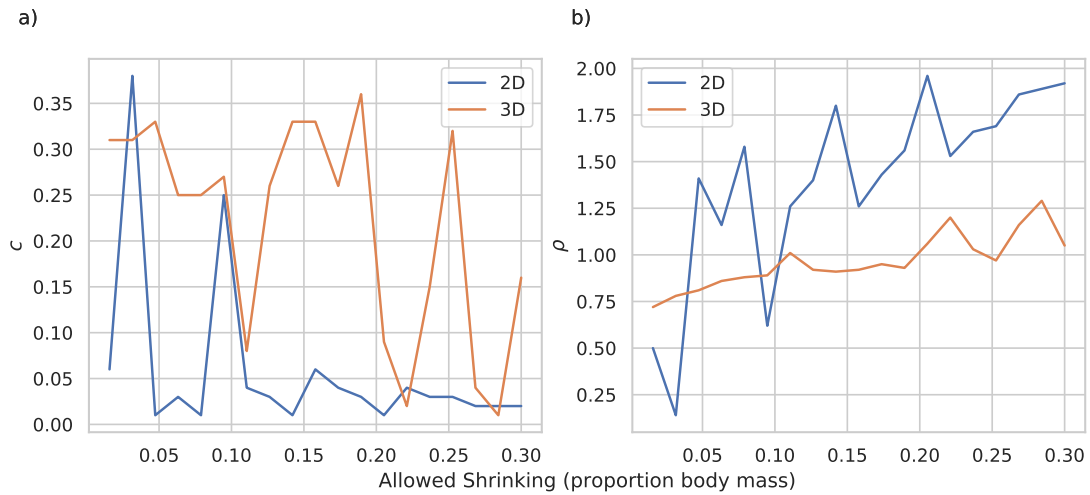


Figure S17: Effect of proportion of shrinking allowed on $c$ and $\rho$ where $\mu = 1$ and resource density is high (100 kg/m$^D$, where $D$ is the dimension).
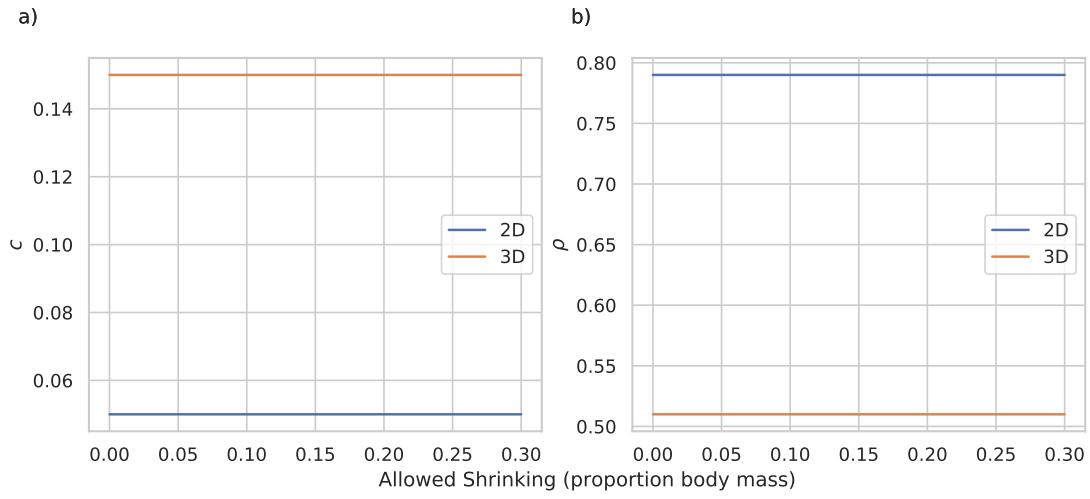
Figure S18: Effect of proportion of shrinking allowed on $c$ and $\rho$ where $\mu = 0.75$ and resource density is high (100 kg/m$^D$, where $D$ is the dimension).