

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

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SUBMITTED: AUGUST 27th 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 ECOLOGY LETTERS

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: 5039

Abstract

Ontogenetic growth models (OGMs) are one of the main model frameworks used to estimate and predict the growth of organisms during ontogeny. However, they make many assumptions which are in conflict with empirical data, in particular resource supply and reproduction. Recent results show that reproduction does not scale allometrically as previously assumed, but rather hyperallometrically. Additionally, not only OGMs but all growth models have failed to properly take variable supply rates into account. They instead assume either optimal or proportions of optimal supply when supply is known not to scale linearly. I develop a model which implements realistic supply scaling and allows for allometric scaling of reproduction. I demonstrate that hyperallometric reproductive scaling is dependent on metabolic scaling and that both are dependent upon supply. This shows that supply is a factor that cannot be ignored when considering growth and reproduction.

Keywords:

allometry; functional response; growth; intake; life history; metabolic theory; metabolism; reproduction; reproductive output; supply

Acknowledgements

I would like to thank my supervisor Dr. Samraat Pawar as well as fellow lab members Tom Clegg and Olivia Moris for giving me so much of their time on weekly, and on occasion more than weekly, basis. I would also like to thank Dr. Diego Barneche for his invaluable feedback and Dr. Van Savage for his assistance with some of the initial model development.

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1 Introduction

Body mass plays a major role in determining many biological factors. For example, larger individuals are less vulnerable to predation, have lower mass specific metabolic rates and produce more offspring in their lifetime (Barneche et al., 2018; Craig et al., 2006; Hixon et al., 2014; Magnhagen and Heibo, 2001; Marshall et al., 2006; Peters, 1983). By extension, knowing the manner in which body mass changes over an organism’s lifetime is the gateway to understanding how many biological rates change throughout ontogeny. The reason for this is that many biological rates scale with mass (Kleiber, 1932). However, despite its importance, relatively little is known about the factors which determine growth trajectories (Arendt, 2011; Marshall and White, 2019).

In the case of fish, understanding growth, and the factors that play a role in determining it, is not only insightful from the perspective of understanding the world around us. It can also be used to better manage the many fisheries and marine protected areas around the world (Heino et al., 2013; Lester et al., 2009), an objective which is becoming increasingly important as the oceans’ fish stocks continue to be depleted by overfishing. The need to understand growth is compounded by global warming which threatens to alter the structure of marine ecosystems even if left unexploited and in their “natural” state (Bruno et al., 2018). It is already known that metabolic rate is dependant on temperature which in turn affects fish sizes (Brown et al., 2004; Gillooly et al., 2001). This, combined with increasing global temperatures, means that understanding in greater detail how increased metabolic rates may affect growth is useful in population management.

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 is 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.

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 is the mass at which growth has essentially stopped due to metabolic cost and energy intake equalling each other (Fig. 1a). The model hinges on the scaling between energy intake ($m^{0.75}$, allometric sub-linear scaling) and maintenance cost (m^1 , isometric linear scaling) with mass. In other words, as mass increases, maintenance costs will slowly overtake the intake rate and halt growth (Fig. 1a). The framework used by West et al. (2001) was later developed by Charnov et al. (2001) to take the cost of reproduction into account and allow the estimation of lifetime production of offspring. Hou et al. (2008) 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 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. Resting metabolic rate is the minimal metabolic rate of an organism and is typically thought of as the metabolic rate of the organism when relaxed and at rest. However, it has been shown, once factors such as movement are taken into account, 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 dependence on asymptotic mass. All other values, such as metabolic cost, are then derived in relation to asymptotic mass and intake rate. However, organisms are not born with an inherent restriction on 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 mass in reality.

Previous OGMs have assumed that reproduction scales isometrically with mass. However, it has been shown that larger fish produce far more offspring than the equivalent mass composed of smaller fish. In other words, a 2kg fish will produce more offspring than two 1kg fish, i.e. reproduction scales hyperallometrically (Barneche et al., 2018). Furthermore, larger fish also use energy more efficiently than multiple smaller ones per unit mass. This is due to their 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). This, combined with empirical results, has led to doubt regarding metabolic scaling. Rather than metabolic scaling being steeper than supply being the cause of growth stopping (Fig. 1a), instead it is thought that the onset of reproduction is what causes growth to cease (Fig. 1b) (Marshall and White, 2019; Sibly and Brown, 2020).

With two key assumptions of current OGMs, that reproduction and metabolism scale isometrically, not holding in the field (Barneche et al., 2018; Peters, 1983), there is a need to take an unexplored approach to modelling growth. This study focuses on developing how intake is described so as to better reflect the real world. To achieve this, a natural 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

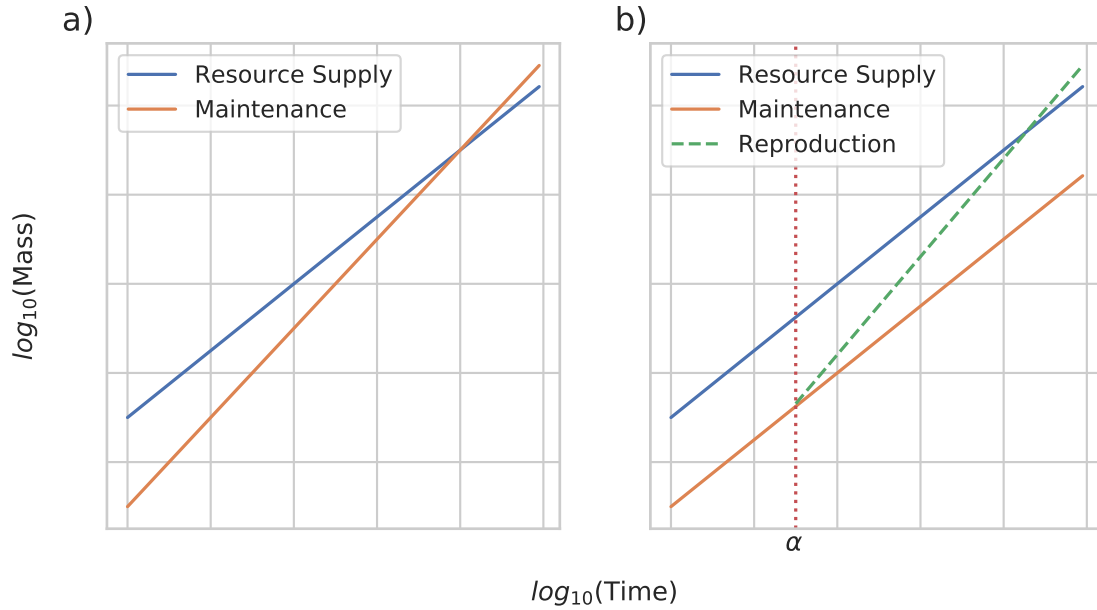


Figure 1: Scaling of intake, maintenance and reproduction with mass over time. The effect of rate scaling exponents can be visualised within log space. The slope of the line is determined by the exponent. a) shows how maintenance cost out-scales supply in a traditional OGM. Growth only stops when maintenance (scaling exponent = 1) reaches the supply line (scaling exponent = 0.75). 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 (α) during development.

less is known about consumption. This necessitates the use of proxy values to estimate intake, 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, since the two are dependent upon each other in current OGMs. This can be achieved 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 as an organism has no concept of “How large should I grow?”, but rather will acquire as much resources as possible at its current life stage and size. Taking this more bottom-up mechanistic approach also allows exploration of factors which control growth, since as previously mentioned, from an energetic standpoint, an organism can grow indefinitely provided there is surplus energy available after costs have been paid. Of course, there are also mechanical and genetic limitations upon organism size. However, once size is constrained to what is known to exist, this is not an issue.

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. This study focuses on supply and growth within fish. However, the same principles can be applied to other taxa.

Assuming that fish have evolved to maximise reproductive output and can adapt to find an optimal strategy within the constraints of resource density, 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 shows that 1) hyperallometric reproduction is dependent upon metabolic scaling exponent, 2) possible scaling of metabolism and reproduction is dependent upon supply and by extension dimensionality.

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 $dm/dt = \text{gain} - \text{loss}$, 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 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)

2.1.1 The Model

The general form of the model still follows that of an OGM, i.e. $dm/dt = \text{gain} - \text{loss}$. The gain term is represented by a functional response ($f(\cdot)$) modified by assimilation efficiency of biomass within poikilotherms (ϵ). Loss is dependent on whether the organism has reached maturity (α) or not. Prior to maturity, loss is resting metabolic rate (B_m) and results in growth as described by Eq. 1. Whereas after maturity, reproductive cost (cm^ρ) starts to be considered, resulting in Eq. 2.

$$\frac{dm}{dt} = \epsilon f(\cdot) - B_m \quad t < \alpha \quad (1)$$

$$\frac{dm}{dt} = \epsilon f(\cdot) - B_m - cm_t^\rho \quad t \geq \alpha \quad (2)$$

2.1.2 Gain

To define supply, 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:

$$f(\cdot) = \frac{aX_r}{1 + ahX_r} \quad (3)$$

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. 3 produces a sigmoidal shape with intake eventually reaching an asymptote after some saturating amount of resources is reached. The

functional response output is in kg/s. Therefore the units are adjusted to kg/d before use in Eq. 1 and 2 (see SI). 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 search rate and handling time can be defined as Eq. 4 and Eq. 5 respectively.

$$a(m) = a_0 m_t^\gamma \quad (4)$$

$$h(m) = t_{h,0} m_t^\beta \quad (5)$$

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 of consumed energy. As a result, to achieve the final gain term, a dimensionless efficiency term ϵ is applied. In poikilotherms assimilation efficiency is roughly 70% (Peters, 1983)

2.1.3 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 takes previously measured values as metabolic cost (see Eq. 6 taken from Peters, 1983 and Table 1 for further details). The output of which requires conversion from J/s to kg/d (see SI).

$$B_m = 0.14 m_t^\mu \quad (6)$$

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^ρ . c can be interpreted as the proportion of mass dedicated to reproduction, i.e. the gonadosomatic index of the fish (Charnov et al., 2001). Just as in Charnov et al. (2001) reproductive cost is only taken into account once maturity is reached. This means that until a length of time (α) has passed, reproductive cost is zero.

2.2 Calculating Fitness

At any time (t) a reproducing organism devotes some amount of energy to reproduction. This is the product of 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; Stearns, 2000;

Vrřílek et al., 2018). In addition to amount of reproduction, 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; Roff, 1993, 2001; Roff, 1984, 1986; Stearns, 1992; Tsoukali et al., 2016)

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

Mortality is experienced differently by juvenile ($t < \alpha$) and reproducing individuals ($t \leq \alpha$) (Day and Taylor, 2018). 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 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 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, $Z \approx 2/\alpha$

2.2.1 Maximising Reproduction

It is assumed that evolution will converge on metabolic values which maximise fitness, with fitness being 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 be solved analytically. 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. 1 and 2) 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; Lambert and Dutil, 2000; Roff, 1983; Wootton, 1985) though c has been shown to reach as much as 0.7 in invertebrate (Parker et al., 2018). To search for any hyperallometry within reproduction, ρ was bound between 0 and 2. The simulation was then run at 0.01 value intervals in both c and ρ 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

181 non-viable if fish had “shrunk” more than 5% in order to accommodate reproductive costs. Shrinking
182 occurs in the model because the combined loss of energy to metabolism and reproduction is too much
183 for the simulated values at the mass achieved by maturation so the individual experiences a deficit
184 of energy, which is paid by loss in mass until equilibrium is achieved. Shrinking is not expected at
185 maturity in reality. Typically, maturity will occur while the organism still has room for growth. It
186 is the onset of reproduction which is considered to slow or stop growth (see Fig. S1). Shrinking can
187 be thought of as starvation in a real organism. If energetic costs are not met, then energy reserves in
188 the body, such as fat and muscle, are broken down for energy. It has been shown that some fish are
189 capable of losing up to 10% of their body mass (Berghe, 1992). However, this was during the breeding
190 season and caused by behavioural changes due to parenting. Additionally, individuals were shown to
191 rebound back to their “normal” body mass once the breeding season had ended.

192 **2.3 Sensitivity Analysis**

193 In order to determine the roles of metabolic exponent, maturation time and resource density within
194 the model, sensitivity analyses were performed on each parameter with regard to c and ρ . This was
195 done by simulating the parameters across multiple values and obtaining the optimal value for c and ρ
196 as described above. The parameter values used in the analysis can be seen in Table 1.

Table 1: 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 represents 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 |
| μ | Metabolic Exponent | - | - | 0.75 - 1.0 | - |
| α | Age of Maturity | 1825 | day | - | - |
| c | Reproduction Scaling Constant | - | kg day^{-1} | 0 - 0.4 | - |
| ρ | Reproduction Scaling Exponent | - | - | 0 - 2 | - |
| Z | Instantaneous Mortality Rate | $2/\alpha$ | - | - | Charnov et al., 2001 |
| k | Reproductive Senescence | 0.01 | - | - | |
| ϵ | Assimilation Efficiency | 0.70 | - | - | Peters, 1983 |
| X_r | Resource Density | - | kg/m^D | 0.11 - 30 | - |
| γ | Search Rate Scaling Exponent | 0.68 (2D) 1.05 (3D) | - | - | Pawar et al., 2012 |
| a_0 | Search Rate Scaling Constant | $10^{-3.08}$ (2D) $10^{-1.77}$ (3D) | $\text{m}^2 \text{s}^{-1} \text{kg}^{-0.68}$ $\text{m}^3 \text{s}^{-1} \text{kg}^{-1.05}$ | - | Pawar et al., 2012 |
| β | Handling Time Scaling Exponent | 0.75 | - | - | Pawar et al., 2012 |
| $t_{h,0}$ | Handling Time Scaling Constant | $10^{3.95}$ (2D) $10^{3.04}$ (3D) | $\text{kg}^{1-\beta} \text{s}$ $\text{kg}^{1-\beta} \text{s}$ | - | Pawar et al., 2012 |

3 Results

3.1 Growth and Maturation

In 3D, when the metabolic scaling exponent (μ) is 1, hyperallometry emerges in reproduction at low resources ,i.e. $\rho > 1$ (Fig. 2b). When resources are high, the value of ρ is lowered (Fig. 2d). This

201 emerges because consumption rate scaling is higher at lower resources in 3D (see Table 1) which allows
202 for steeper scaling within reproduction. This same pattern occurs within 3D for $\mu = 0.75$ (Fig. 3).

203 In 2D, the opposite pattern is seen for $\mu = 0.75$, with ρ at low resources lower than at saturated
204 resources (Fig. 3a, c). This can again be explained by the difference within supply scaling at high
205 vs. low resources in 2D, since supply scaling is greater at high resources than at low resources in 2D.
206 However, when $\mu = 1$ in 2D, this pattern is reversed (Fig. 2a, c). This may be caused by the very
207 small amount of reproduction occurring at low resources, but if this were the case, the same pattern
208 would be expected to be seen for $\mu = 0.75$, which is not the case. As resources increase, but still
209 remain low, ρ does drop below that of the value at high resources, before climbing back up. However,
210 the relationship is not clear (see Fig. S12 and S14)

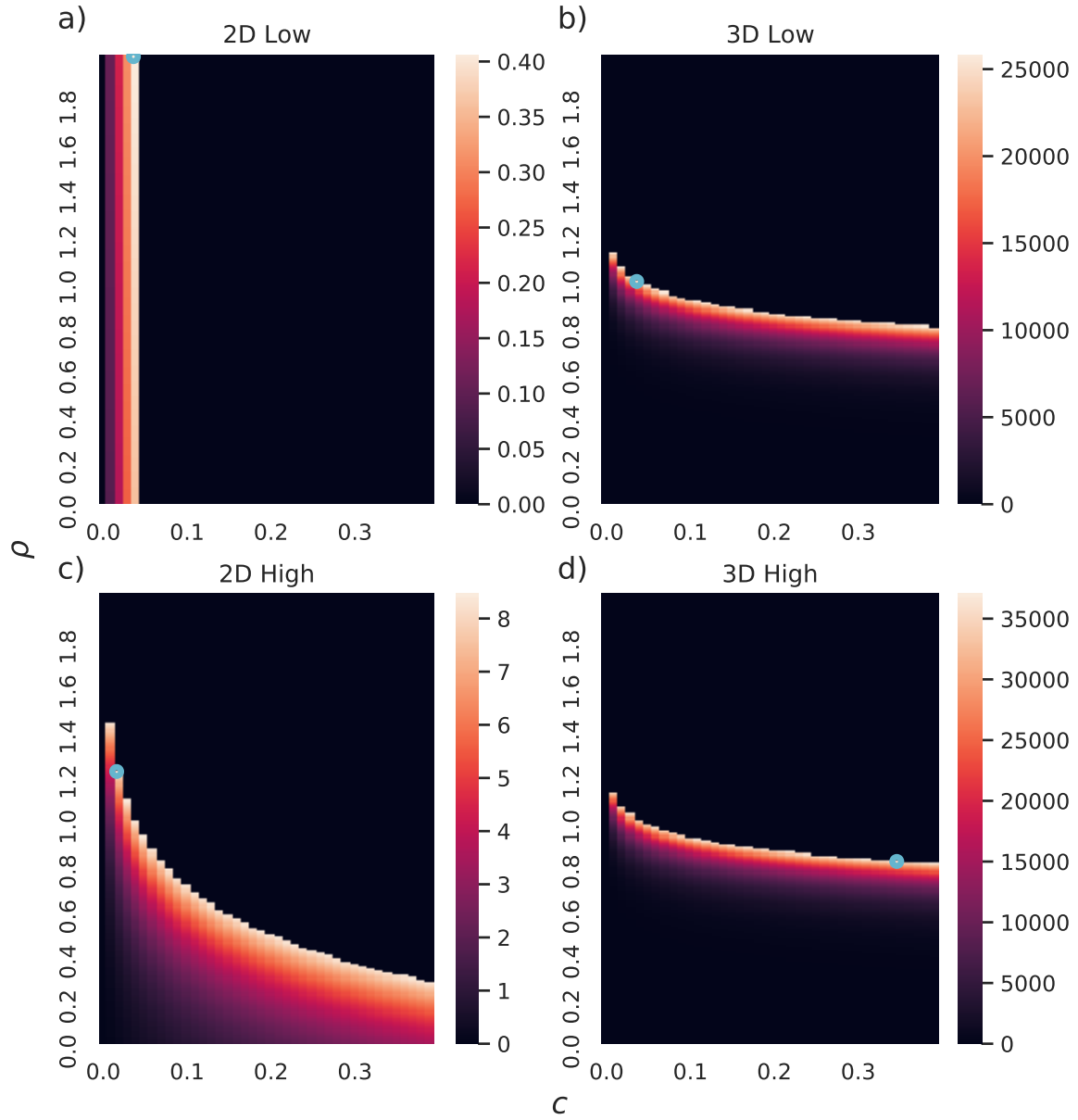


Figure 2: Metabolic exponent of 1 in 2D vs 3D at high and low resource densities. The optimal value is denoted by the blue circle. The resources used for the low resource scenario (top row) is the minimum amount of resources that allows growth with a c and ρ of 0.01. As would be expected, since scaling is steeper in 3D, it allows for growth at smaller resource densities than 2D. Low resources in 2D were $\approx 0.11\text{kg/m}^2$ and 0.00035kg/m^3 in 3D. 100kg/m^D , where D is dependent on dimension, 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 at high (c) and low resources (a). Scaling in 3D is hyperallometric at low resources (b) and hypoallometric at high resources (d). Intensity of colour is determined by reproductive output in kg/s.

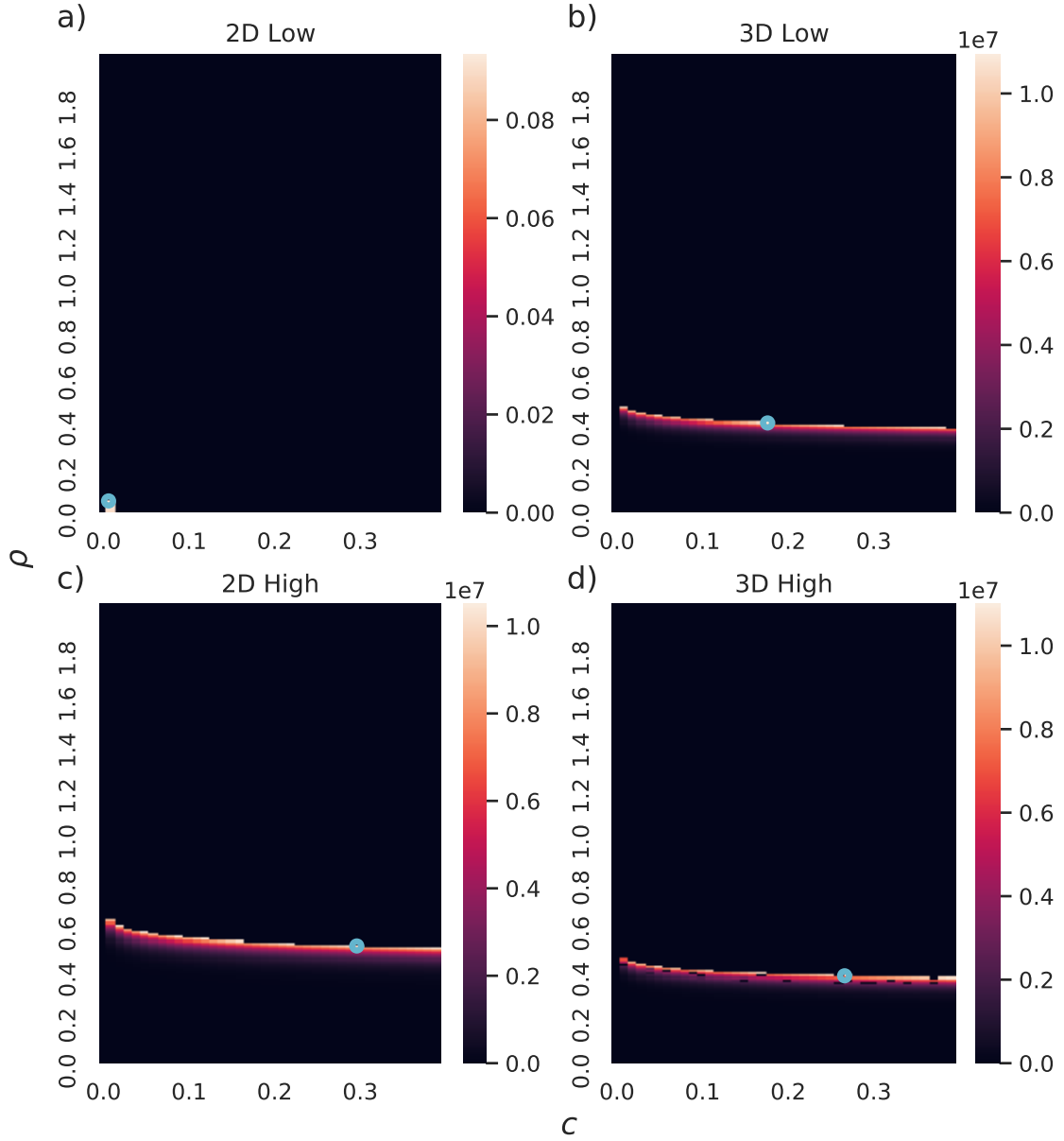


Figure 3: Metabolic exponent of 0.75 in 2D vs 3D at high and low resource densities. The optimal value is denoted by the blue circle. The resources used for the low resource scenario (top row) is the minimum amount of resources that allows growth with a c and ρ of 0.01. As would be expected, since scaling is steeper in 3D, it allows for growth at smaller resource densities than 2D. Low resources in 2D were $\approx 0.11\text{kg/m}^2$ (a) and 0.00035kg/m^3 in 3D (b). 100kg/m^D , where D is dependent on dimension, was used for high resources because, which although unrealistic, ensures that resources are not a limiting factor in the simulations (c, d). Hypoallometric scaling is observed in all cases. Intensity of colour is determined by reproductive output in kg/s.

3.2 Sensitivity Analysis

3.2.1 Resource Density

The scaling relationship of ρ 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 (see Table 1), as resources increase and the response shifts to scaling similarly to the inverse of handling time. At this point ρ starts to take values which are higher in 2D than 3D, because of the higher normalisation constant in 2D.

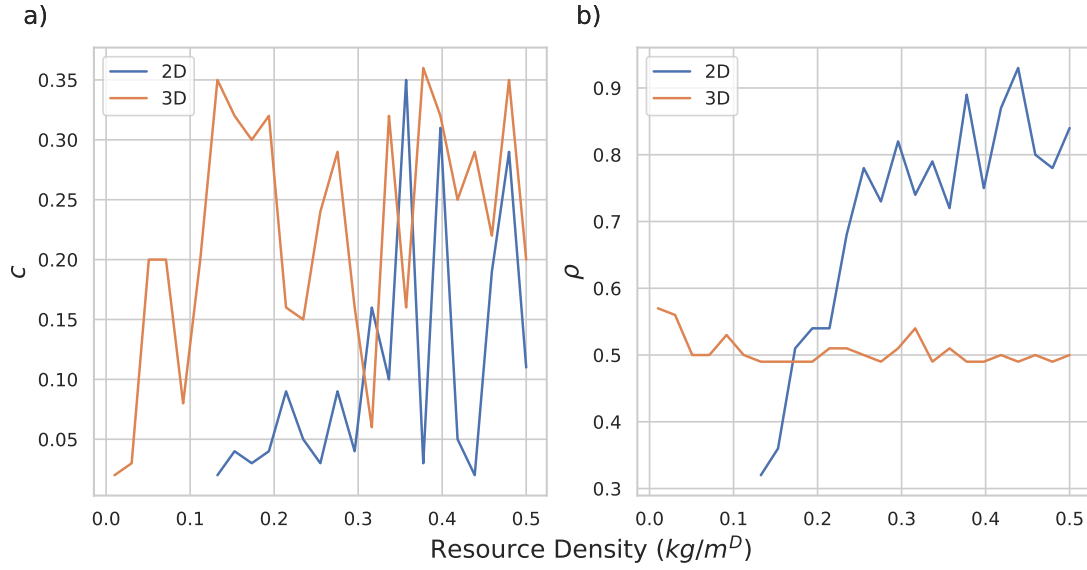


Figure 4: Effect of resource density on c and ρ where $\mu = 0.75$. Demonstrates the expected trend that under limiting resources, the higher scaling of 3D search rate allows for steeper reproductive scaling (Table 1). As resources increase and supply shifts more towards being defined by the inverse of handling time, steeper scaling in 2D allows for higher ρ values. Units are kg/m^D , where D is the dimension.

3.2.2 Metabolic Exponent

The expected result is for increasing values of μ for ρ to also increase. This is because the lower values of μ will result in there being a larger gap between the scaling of intake and maintenance, which allows for steeper scaling in reproduction (see Fig. 1b) (Marshall and White, 2019). However, the trend suggests that increasing μ allows for higher values of ρ . This is due to numerical instability for greater values of ρ .

3.2.3 c Values

Estimations of c are low in some cases, especially in 2D (for example Fig. S5 and Fig. S18). While this may be low compared to the $\sim 10\%$ - 35% expected (Benoît et al., 2018; Fontoura et al., 2009; Roff, 1983; Wootton, 1985), 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.

3.2.4 Shrinking

When $\mu = 1$, increasing proportions of shrinking allows for higher values of ρ . This is with the exception of low resources in 2D (Fig. S17). This is because at limited resources, with scaling that is lower than that of μ , there is no leeway for steeper scaling of reproduction. In contrast, at very low resources in 3D, increased shrinking does allow for steeper reproductive scaling (Fig. S19), because of the steeper scaling in supply (Table 1).

When $\mu = 0.75$, larger proportions of shrinking has no effect. This is because supply scaling is equal to or greater than μ in all cases, meaning greater shrinking does not create “space” for ρ to scale steeper. The exception to this is at low resources in 2D (Fig. S18), where some effect is seen because of the low scaling of intake at low resources in 2D (Table 1).

4 Discussion

This study shows that resource supply plays a critical role in determining the growth and reproductive output of an organism. I show that reproductive scaling (ρ) is not only dependent upon resource density, but whether feeding occurs in two or three dimensions. I demonstrate that hyperallometry can emerge in reproduction, both in 2D and 3D (Fig. 2). The hyperallometry arises with the use of empirically derived values of resource supply, not just maximal intake as in past studies (e.g. West et al. (2001), Hou et al. (2008)). Values of ρ which yielded the highest fitness ranged from slightly hypoallometric (Fig. 2b), to around 1.3 as predicted by Barneche et al. (2018) (Fig. 2c), to extremely hyperallometric (Fig. 2a). The hyperallometry indicates that there is a need to reconsider current fishing practices which prioritise larger fish and lead to a greater proportion of smaller fish in populations (Heino et al., 2013), as under hyperallometric scaling larger individuals will produce more offspring per unit mass than smaller ones. The hyperallometry shown in Fig. 2 is when the metabolic scaling exponent (μ) is 1. The results shown in Fig. 3 indicate that reproduction is hypoallometric when μ is 0.75. This is contrary to what should happen theoretically, since the larger “space” between metabolism and supply allows for higher values of ρ . However, these results are misleading. The equal scaling of metabolism and resource supply results in rapid growth which does not slow down without other additional costs. When reproduction is introduced at such high masses ($m > 3 \times 10^{17}$), the system becomes extremely unstable. Accordingly, the result cannot be taken as a “reasonable” growth trajectory and is discounted. Sensitivity analysis of maturation time shows that when maturation is early, which effectively restricts growth, steeper reproductive scaling is possible numerically (e.g. Fig. S4), however more investigation is required. The sensitivity analysis also highlights scenarios in which shrinking can lead to steeper reproductive scaling. Prior to maturity, metabolism and supply can be scaling parallel to each other (Fig. 1b) or towards each other (Fig. 1a). At maturity, shrinking has

the effect of allowing mass to decrease, and for growth to effectively reverse. This opens more “space” for reproduction to be steeper causing gain and loss to equal each other at the smaller mass (Fig. 1b). When scaling of supply and metabolism are equal, the decrease in mass has no effect. However, if maintenance has steeper scaling than supply then shrinking allows for larger values of ρ .

Growth within the model is fast, with asymptotic mass being reached within ~ 10 days (Fig. S3 - S8). 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 parameterisation 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. 1). As such, inclusion of active metabolic rates, while challenging to measure directly and implement, is needed. It is also possible that active costs will not scale constantly for all sizes of fish, as larger individuals incur less drag in the water than smaller ones (Müller et al., 2000). Taking the above factors into account would result in a greater metabolic cost from birth. This would reduce the speed of growth and likely resolve the numerical instability within this studies results of this model at low μ values.

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 alters 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 been shown to 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

299 be improved (Marshall and White, 2019).

300 A factor that is not taken into account in this model is that resources are not constant over time.
301 This can be implemented by varying resource density over time. The functional response will respond
302 accordingly giving intake which varies through time. One concern with implementing such a response
303 is fluctuations are not experienced by all organisms in the same way. For a fish with a small range,
304 a local fluctuation can be measured and described relatively simply. However, for a fish with a very
305 large range, there is the possibility of leaving resource poor areas in search of richer waters. The speed
306 at which growth occurs in the model limits comparisons and testing that can be done with lab or field
307 data. However, the scaling relationships and patterns demonstrated here remain true.

308 In conclusion, this study demonstrates the need for more consideration for resource supply within
309 growth models. Additionally, I provide direction where the model can be expanded upon that was
310 not possible with OGMs, allowing for much more controlled and detailed explanations of the factors
311 controlling growth. In contrast to all previous work, which assume optimal supply, the concept of
312 varying supply is addressed using functional responses. Additionally, qualitative evidence is provided
313 supporting hyperallometric scaling in fish using energy budget as the basis. The model can easily be
314 applied to any animal taxon, not just fish, with some simple changes. Furthermore, there are clear
315 directions to be explored in order to improve the model's accuracy.

316 **Code and Data Availability**

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

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450 Supplementary Information

451 4.1 Unit Conversions

452 4.1.1 Functional Response ($f(\cdot)$)

$$kg \cdot s^{-1} \cdot 24 \cdot 60 \cdot 60 = kg \cdot d^{-1} \quad (S1)$$

453 4.1.2 Metabolic Cost (B_m)

Conversion factor for joules to kg wet mass from Weathers et al. (2012).

$$J \cdot s^{-1} \cdot 24 \cdot 60 \cdot 60 = J \cdot d^{-1} \quad (S2)$$

$$J \cdot d^{-1} \cdot 2.5 \times 10^{-4} = kg \cdot d^{-1}$$

454 4.2 Growth Curves

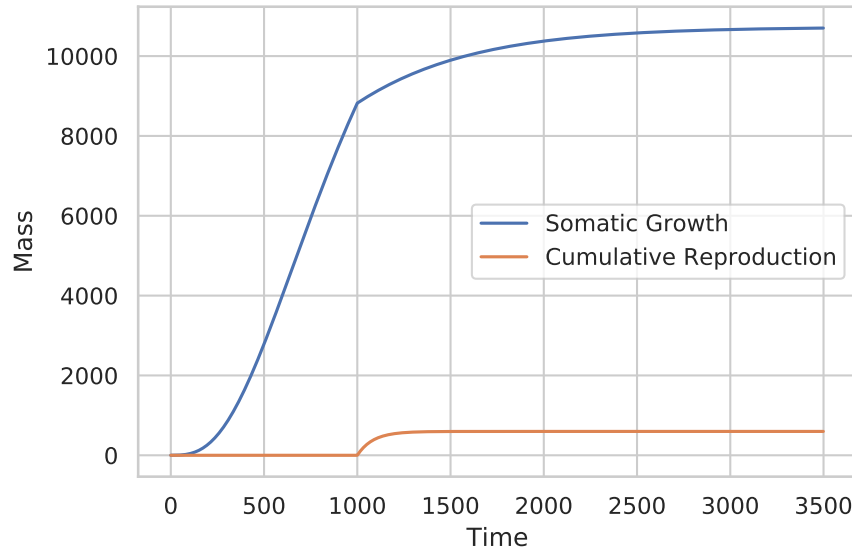


Figure S1: Example of the growth curve and cumulative reproduction expected from a traditional OGM model. Maturation occurs at 1000 days, after which growth is less steep until reaching asymptotic mass.

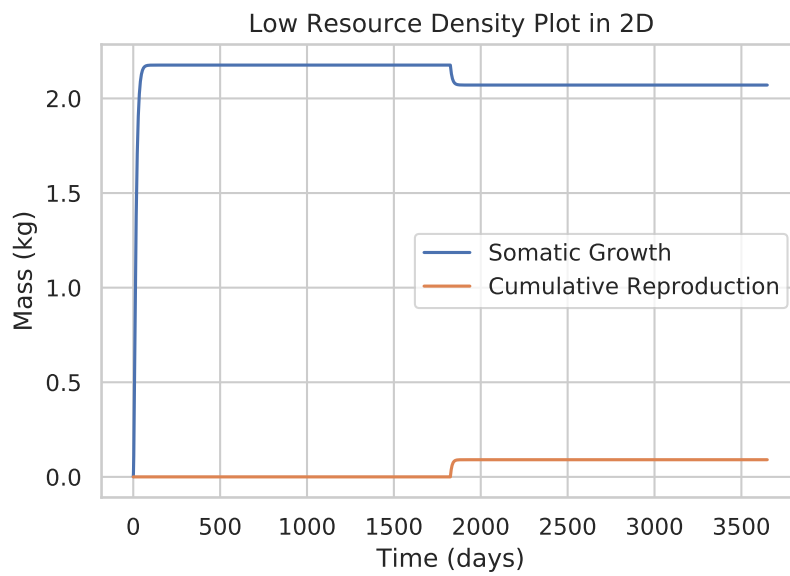


Figure S2: The growth over a fish which consumes in 2D. Maturation occurs at 5 years (1825 days). The fish was allowed to shrink by 5% at the onset of reproduction.

4.3 Sensitivity Analysis

4.3.1 Maturation Time

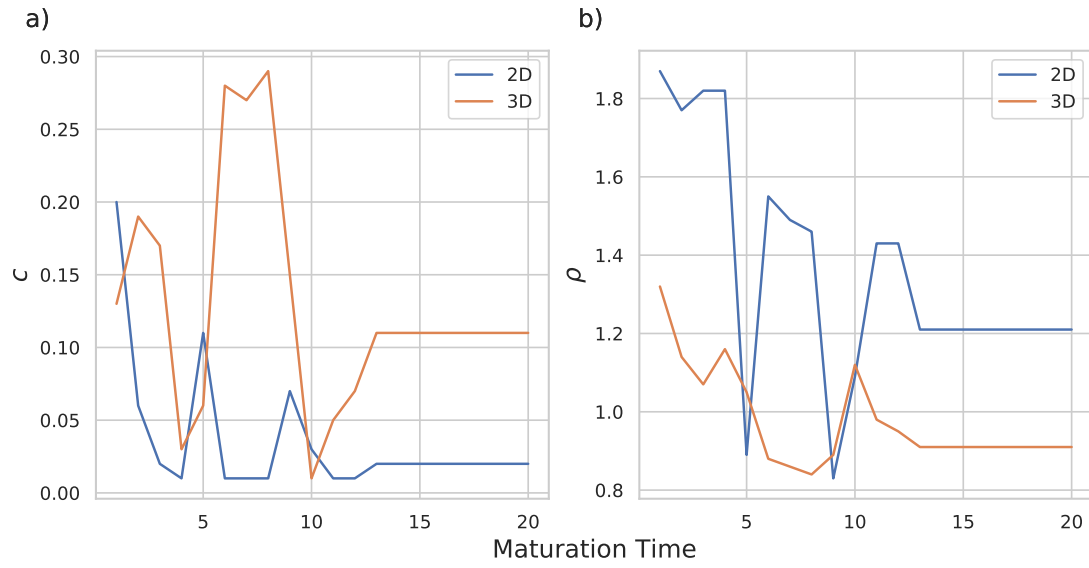


Figure S3: Effect of maturation time on c and ρ where $\mu = 1$ and resource density is high (100 kg/m^D, where D is the dimension).

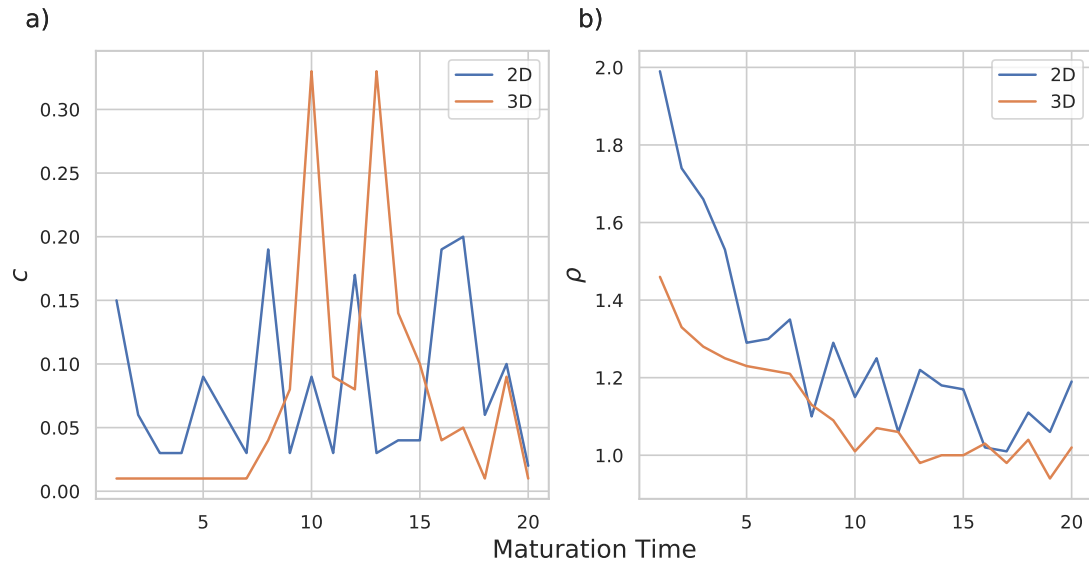


Figure S4: Effect of maturation time on c and ρ where $\mu = 0.75$ and resource density is high (100 kg/m^D, where D is the dimension).

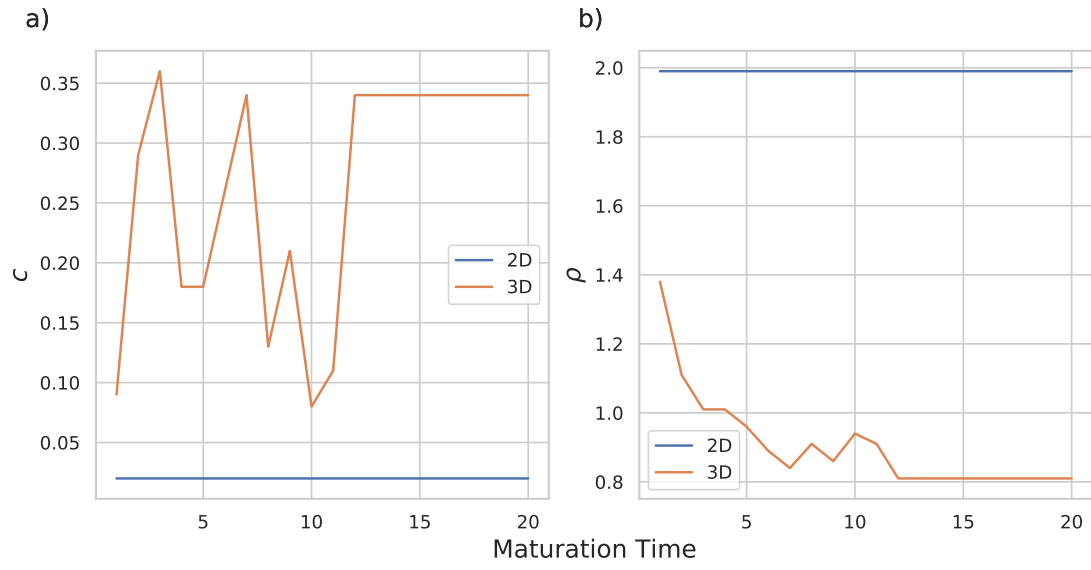


Figure S5: Effect of maturation time on c and ρ where $\mu = 1$ and resource density is low (0.11 kg/m^D, where D is the dimension).

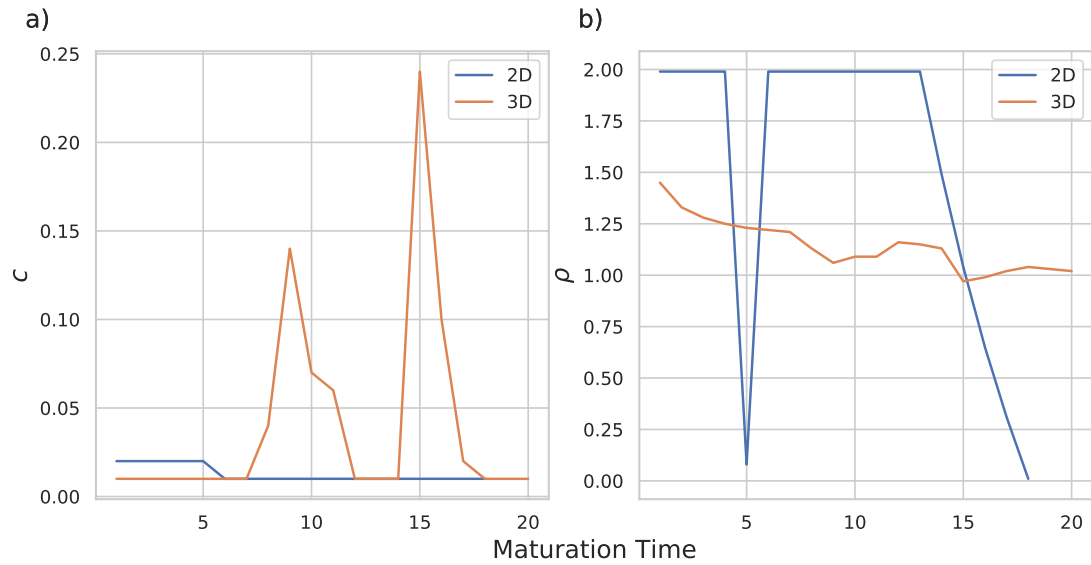


Figure S6: Effect of maturation time on c and ρ where $\mu = 0.75$ and resource density is low (0.11 kg/m^D, where D is the dimension).

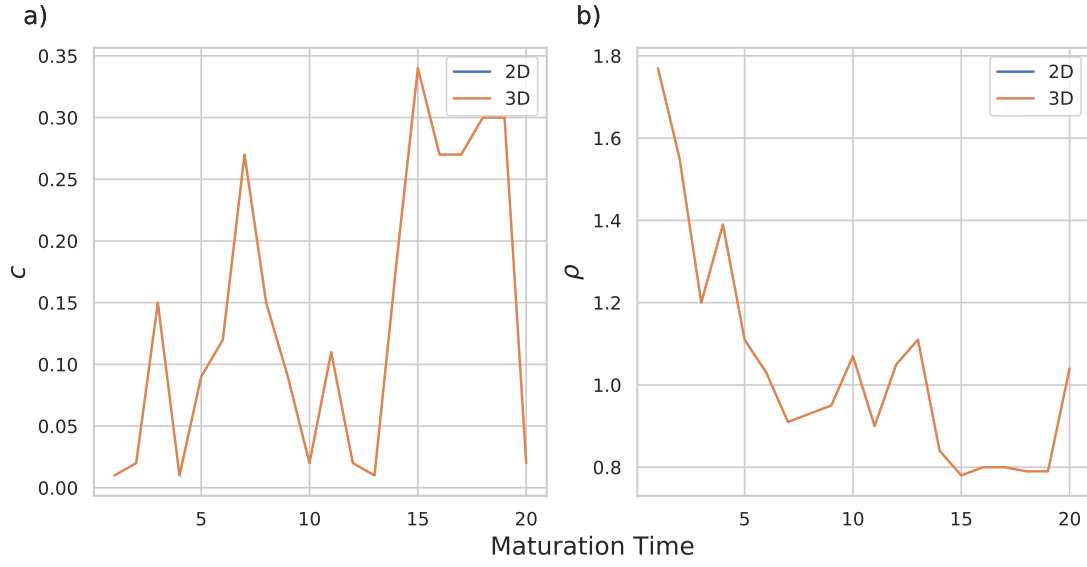


Figure S7: Effect of maturation time on c and ρ where $\mu = 1$ and resource density is very low (0.01 kg/m^D , where D is the dimension). At this resource density reproduction can only occur in 3D.

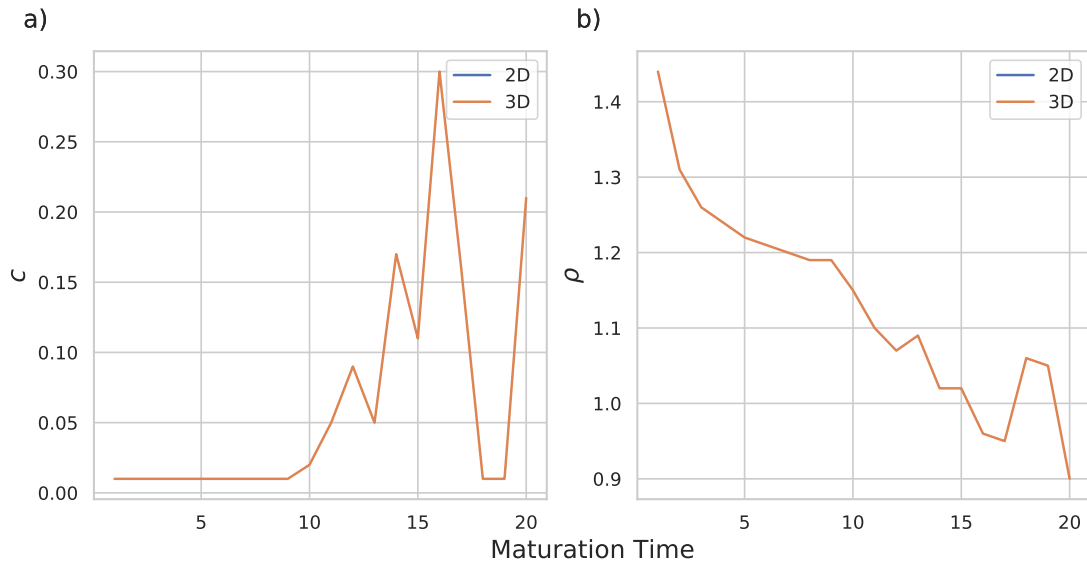


Figure S8: Effect of maturation time on c and ρ where $\mu = 0.75$ and resource density is very low (0.01 kg/m^D , where D is the dimension). At this resource density reproduction can only occur in 3D.

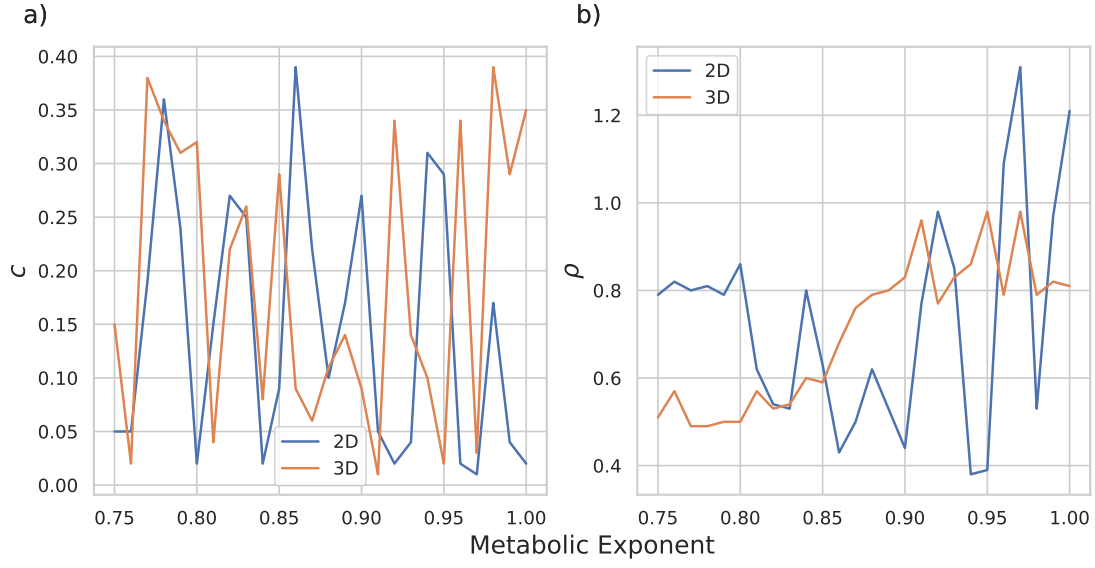


Figure S9: Effect of metabolic on c and ρ where resource density is high (100 kg/m^D, where D is the dimension)

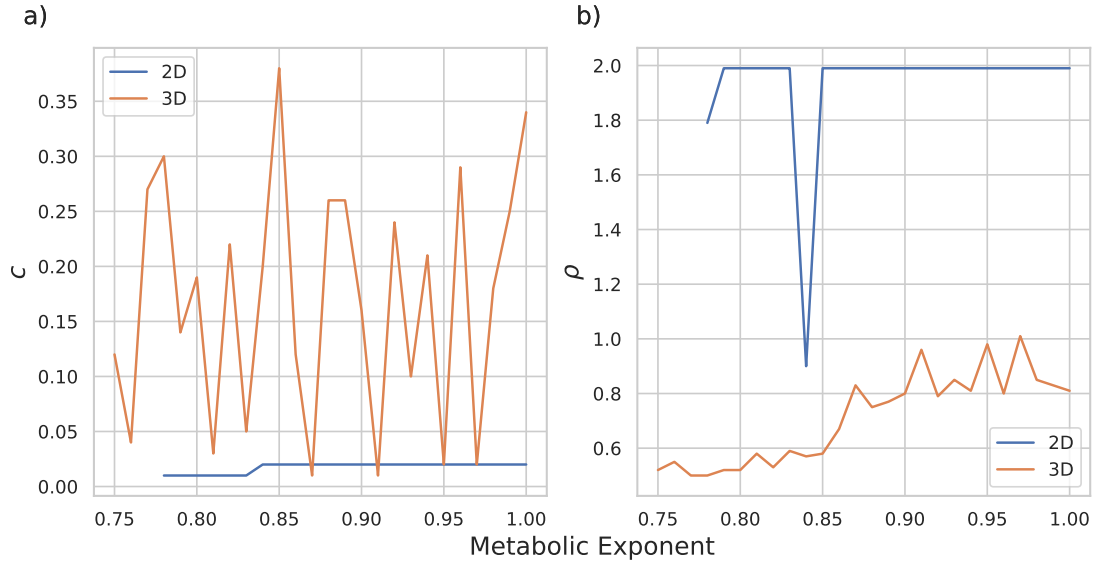


Figure S10: Effect of metabolic on c and ρ where resource density is low (0.11 kg/m^D, where D is the dimension)

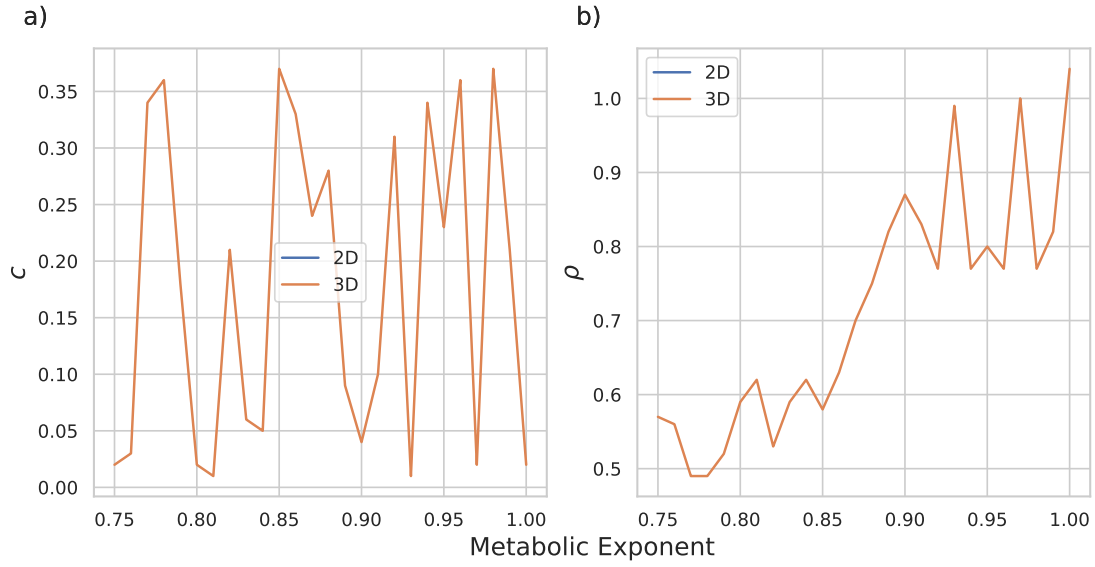


Figure S11: Effect of metabolic on c and ρ where resource density is very low (0.01 kg/m^D , where D is the dimension). At this resource density reproduction can only occur in 3D.

458 4.3.3 Resource Density

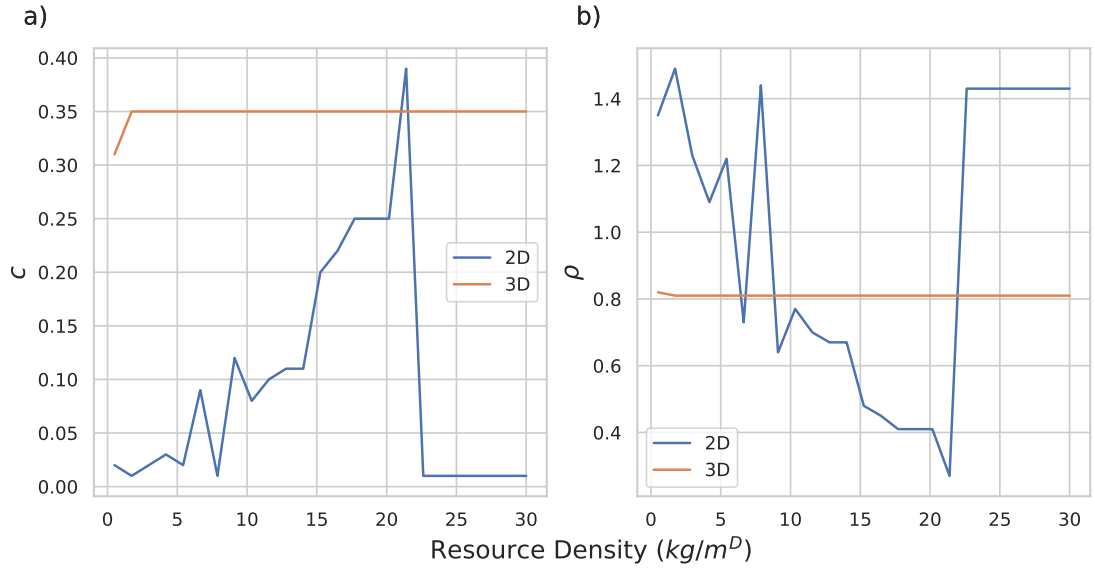


Figure S12: Effect of resource density on c and ρ where $\mu = 1$. Over larger values for resource density. 3D quickly saturates at this density, thus is a nearly straight horizontal line. See Fig. 4 for detail at lower resource density. Units are kg/m^D , where D is the dimension.

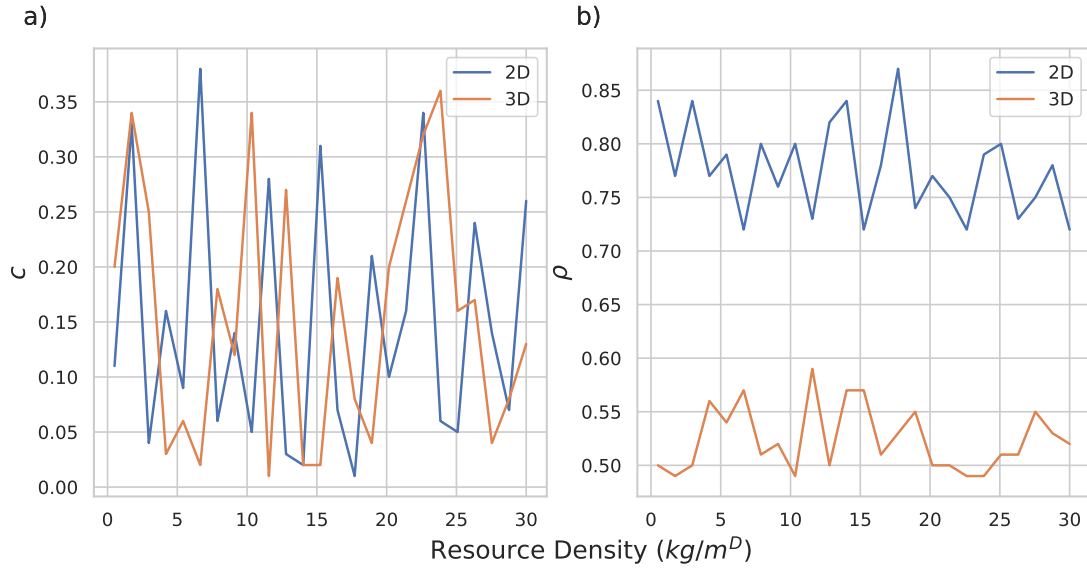


Figure S13: Effect of resource density on c and ρ where $\mu = 0.75$. Over larger values for resource density. There is a lot of numeric instability across resource densities, but the trend appears to be somewhat stable around ~ 0.8 in 2D and ~ 0.53 in 3D See Fig. 4 for detail at lower resource density. Units are kg/m^D , where D is the dimension.

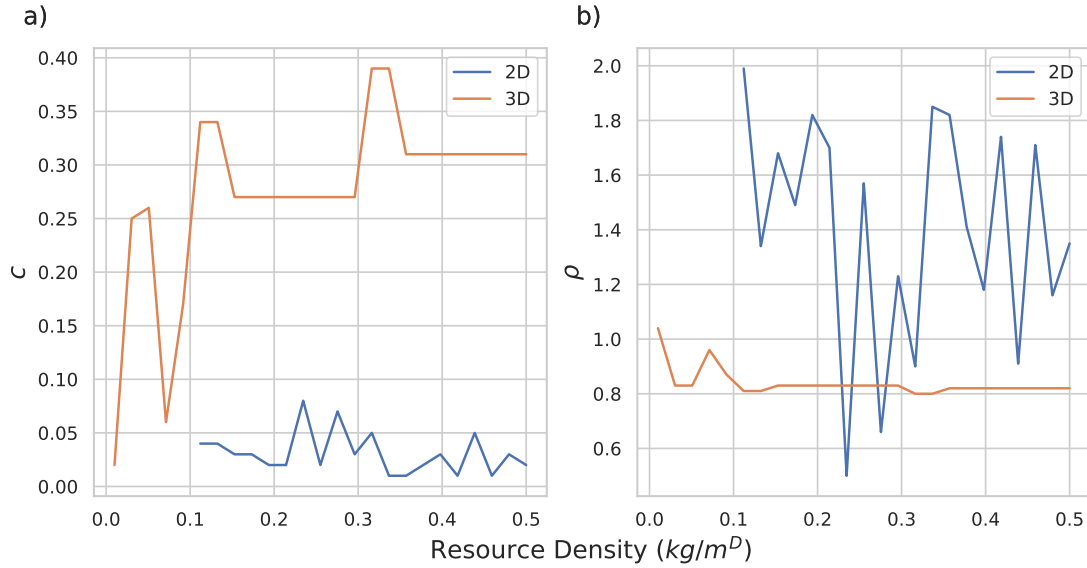


Figure S14: Effect of resource density on c and ρ where $\mu = 1$. Demonstrates the expected trend that under limiting resources the higher scaling of 3D search rate allows for steeper reproductive scaling (Table 1). As resources increase and supply shifts more towards being defined by the inverse of handling time, steeper scaling in 2D allows for higher ρ values. Units are kg/m^D , where D is the dimension.

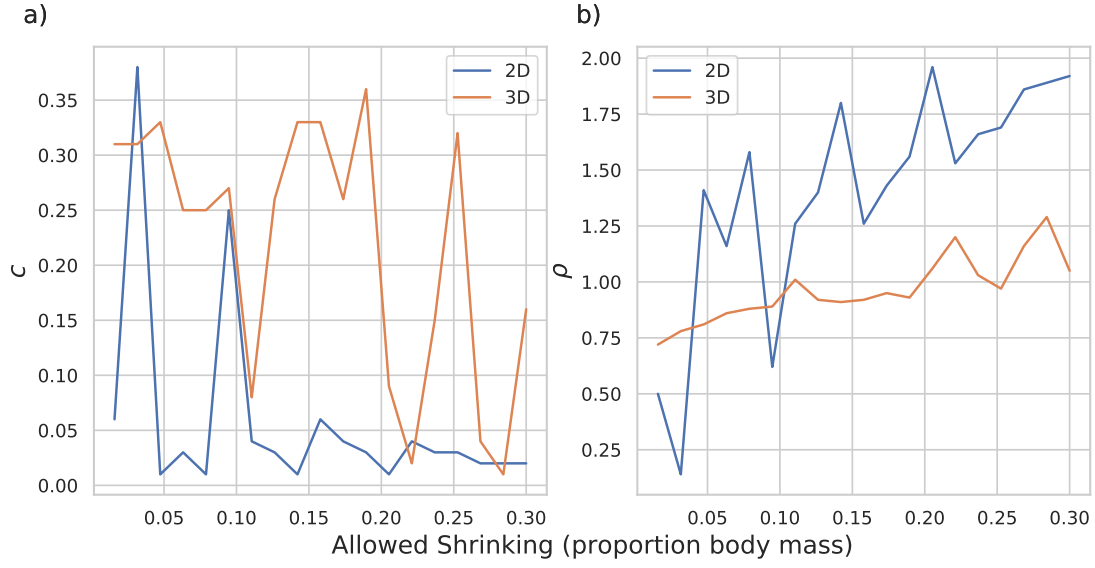


Figure S15: Effect of proportion of shrinking allowed on c and ρ where $\mu = 1$ and resource density is high (100 kg/m^D , where D is the dimension).

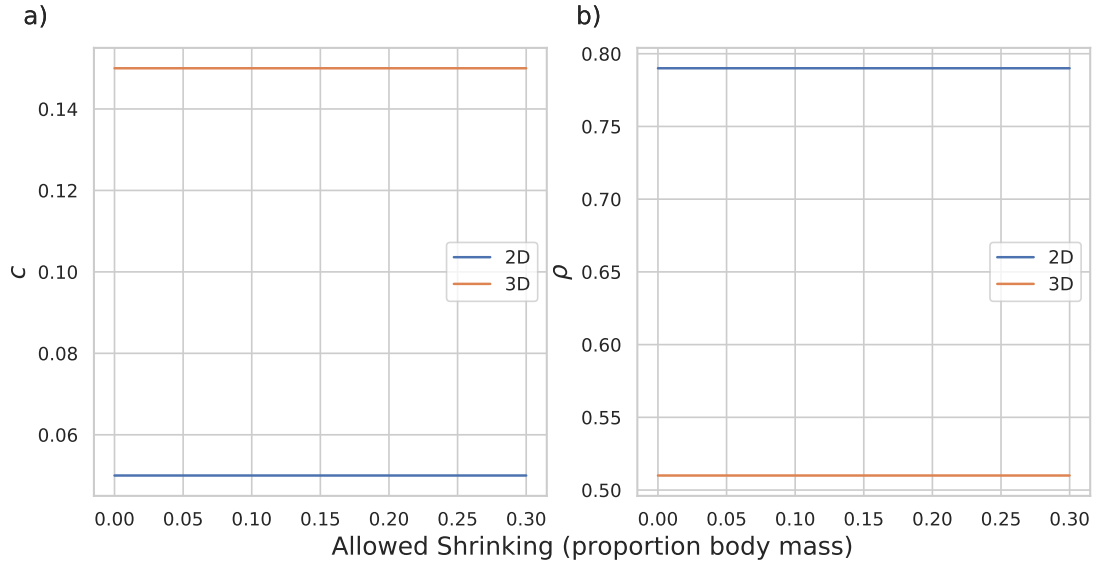


Figure S16: Effect of proportion of shrinking allowed on c and ρ where $\mu = 0.75$ and resource density is high (100 kg/m^D , where D is the dimension).

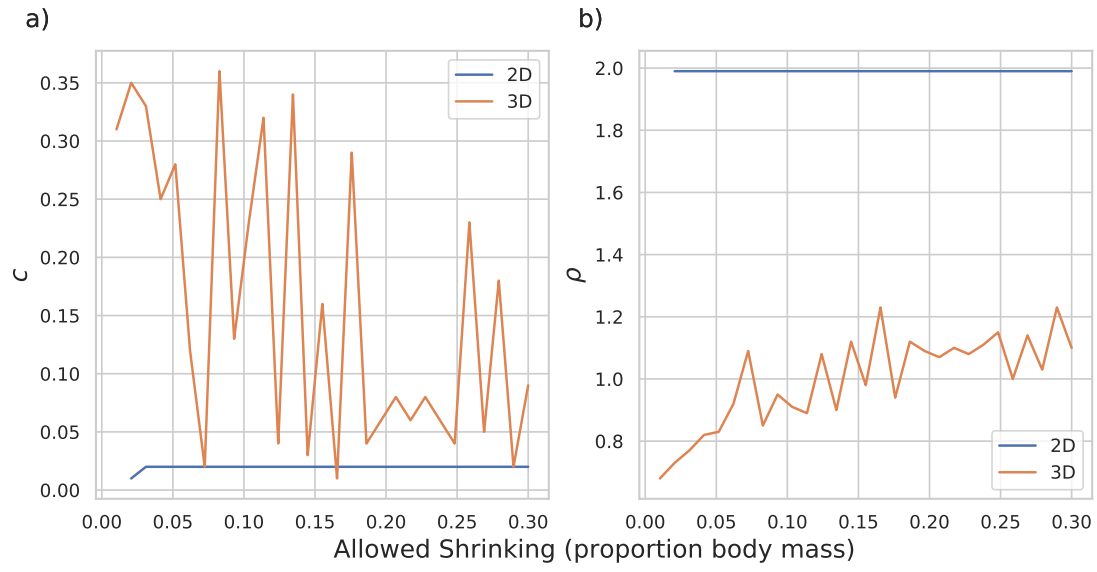


Figure S17: Effect of proportion of shrinking allowed on c and ρ where $\mu = 1$ and resource density is low (0.11 kg/m^D , where D is the dimension)

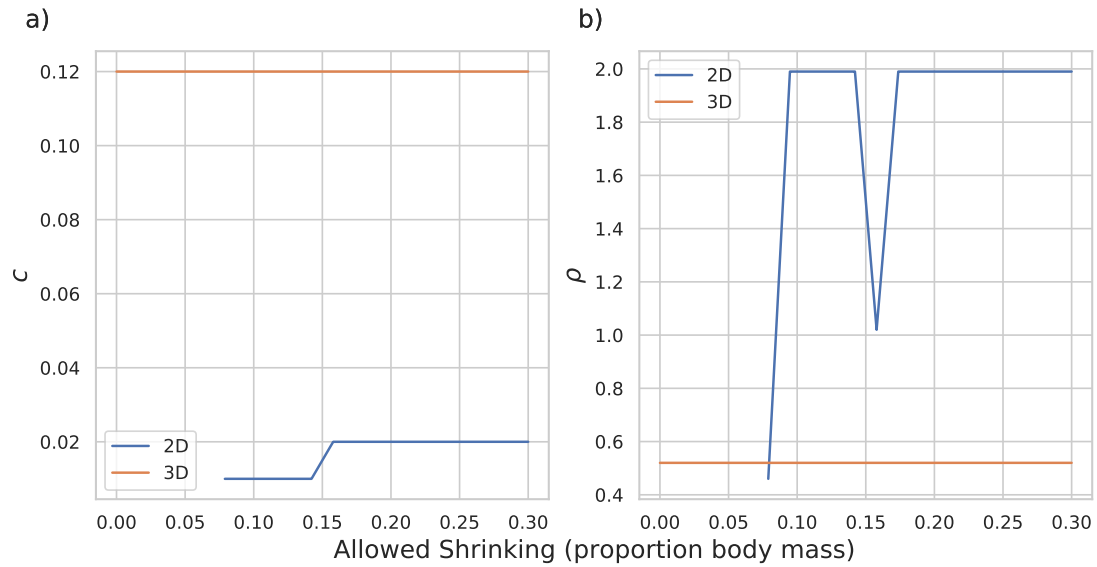


Figure S18: Effect of proportion of shrinking allowed on c and ρ where $\mu = 0.75$ and resource density is low (0.11 kg/m^D , where D is the dimension)

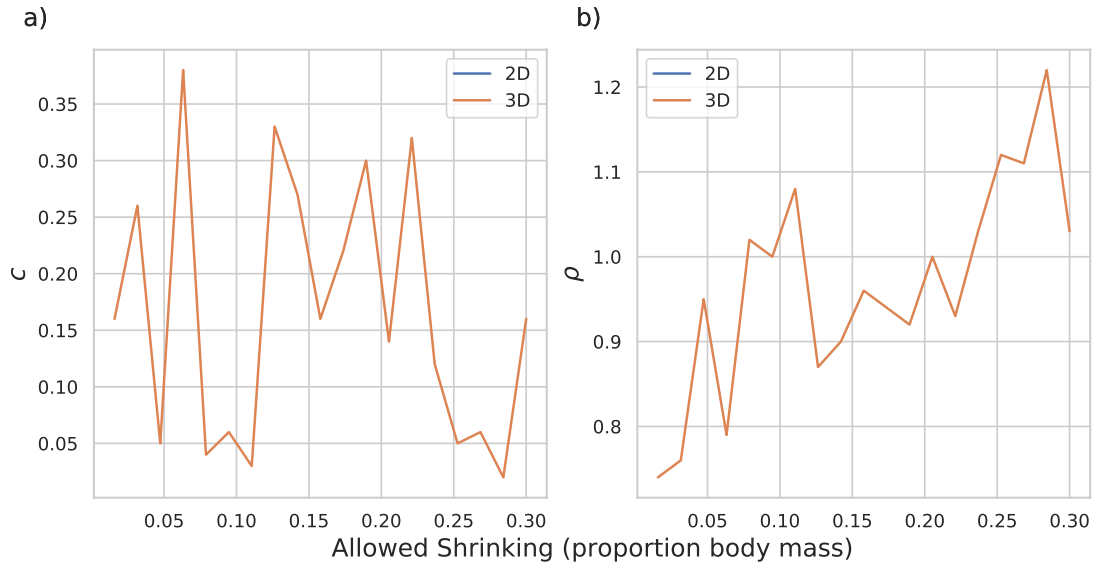


Figure S19: Effect of proportion of shrinking allowed on c and ρ where $\mu = 1$ and resource density is very low (0.01 kg/m^D , where D is the dimension). The resource density only allows for reproduction to occur on 3D.

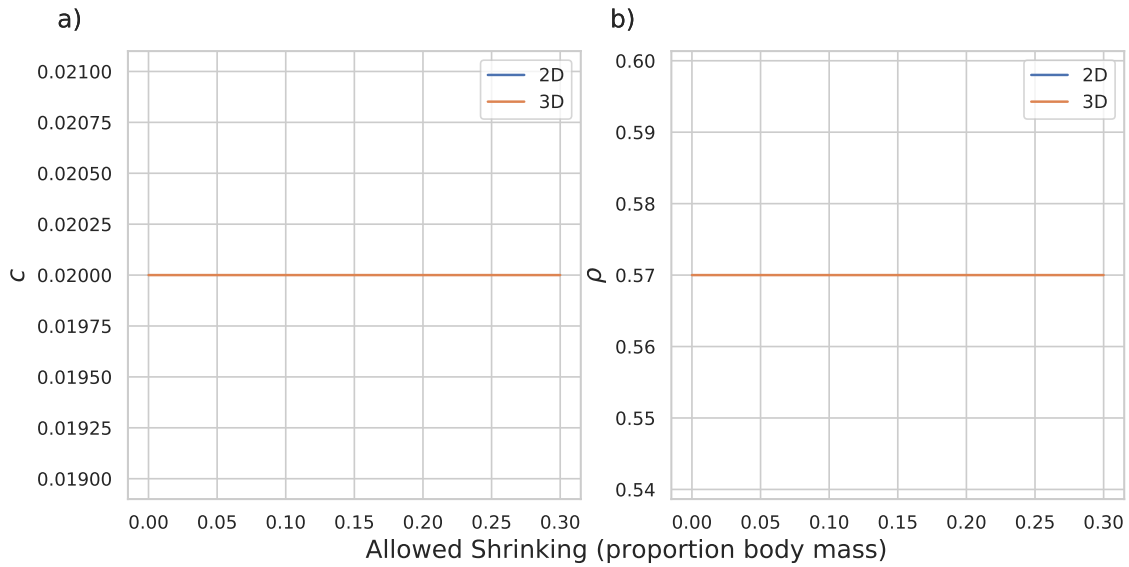


Figure S20: Effect of proportion of shrinking allowed on c and ρ where $\mu = 0.75$ and resource density is very low (0.01 kg/m^D , where D is the dimension). The resource density only allows for reproduction to occur on 3D.

460 **References**

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