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# ENERGY INVESTMENT IN GROWTH RATE AND REPRODUCTION

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## Abstract

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# 1 Introduction

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

Larger fish produce more offspring than smaller ones. In fact, it has been shown that larger fish produce far more offspring than the equivalent mass composed of smaller fish, That is a 2kg fish will produce more offspring than two 1kg fish (Barneche et al. 2018). Larger fish also use energy more efficiently than multiple smaller ones per unit mass. This is due to them having a lower mass specific metabolic rate (Brown 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 rates 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.

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

Another approach has been to try explain growth from an energetic perspective. That is an individuals growth is determined by the amount of energy available to it. Once all costs, such as maintenance, have been paid all remaining energy can be invested towards growth. There are two frameworks which have been built around this concept; dynamic energy budget (DEB) theory and

35 ontogenetic growth models (OGMs), which will be focused on here.

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

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

49 In the above OGMs intake is assumed to scale sub-linearly to the power of 0.75. This is due to the  
50 assumption that the individuals are consuming at an optimal rate at all times and therefore the only  
51 limitation is their ability to make use of that energy. In this case, intake should theoretically scale to  
52 the power of 0.75 (see West et al. 1997). However, this is not always the case in the field. It has been  
53 shown that, for non-optimal consumption, steeper scaling can occur (Pawar et al. 2012; Peters 1983).  
54 Additionally, OGMs, like many growth and metabolic models, typically use basal or resting metabolic  
55 rate to calculate metabolic cost. This is the minimal metabolic rate of an organism and is typically  
56 thought of as the rate of the organism when at relaxed and at rest. However, it has been shown,  
57 once factors such as movement are taken into account, that the scaling becomes steeper (Weibel et al.  
58 2004). The issue of non-optimal feeding is addressed somewhat by Hou, Bolt, et al. (2011). However,  
59 this growth was only investigated as, essentially, a proportion of optimal consumption and does not  
60 address a potential change in scaling of intake rate. Another limitation of the models used in previous  
61 OGMs is the dependence on asymptotic mass. The models are entirely dependant on the value of  
62 optimal intake and asymptotic mass. All other values, such as metabolic cost, are then derived in  
63 relation to these. However, organisms are not born with some inherent restriction to the size they  
64 can attain, at least not energetically. If there is surplus energy for a given mass the organism should  
65 be able to grow. Relying on asymptotic mass to define the upper bound of attainable mass does not  
66 allow for investigation of the mechanisms that underpin asymptotic size in reality.

67 With two of the key assumptions of current OGMs, that reproduction and metabolism scale iso-  
68 metrically, not holding in the field (Barneche et al. 2018; Pawar et al. 2012; Peters 1983) there is a need  
69 to take an unexplored approach to modelling fish growth, in particular choosing to focus on developing  
70 how intake is described so as to better reflect the real world. To do this an obvious starting point is

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

## 2 Methods

### 85 2.1 Gain

#### 86 2.1.1 Search Rate

#### 87 2.1.2 Handling Time

#### 88 2.1.3 Functional Response

### 89 2.2 Loss

#### 90 2.2.1 Maintenance Cost

#### 91 2.2.2 Reproductive Cost

### 92 2.3 Reproductive Output

## 3 Results

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

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

94 Multiplot with 2D vs 3D and changing exponents, likely range from 0.75 to 0.85

95

## 4 Discussion

## 5 Conclusion

### Code and Data Availability

Code is available at: [https://github.com/Don-Burns/Masters\\_Project](https://github.com/Don-Burns/Masters_Project)



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## Supplementary Information

### 5.1 notes

need section on value conversions and derivations