

REALISTIC INTAKE RATE SCALING ALLOWS FOR
HYPERALLOMETRIC FECUNDITY RATE AND
LATER MATURITY IN FISH

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Declaration of Originality

I certify that this thesis, and the research to which it refers, are the product of my own work, conducted during the current year of the *M.Sc. Computational Methods in Ecology & Evolution* at Imperial College London. Any ideas or quotations from the work of other people, published or otherwise, or from my own previous work are fully acknowledged in accordance with the standard referencing practices of the discipline and this institution. I digitised and processed caloric equivalents data from Cummins & Wuycheck (1971) and Steimle & Russell (1980). I developed the mathematical models presented in this paper equally with my supervisor, Dr Samraat Pawar, and Ph.D. student, Tom Clegg.

Luke Joseph Vassor
August 29, 2019

Abstract

The amount of metabolic energy an organism can sequester from its environment fundamentally determines its scope for growth and reproduction. Here I use a fish-based bioenergetics and life history theoretical model, which optimises fecundity parameters, to show that an instantaneous rate of allocation to fecundity is unlikely to scale hyperallometrically (increase disproportionately) with mass under traditional intake rate values. I further show that using an arguably more realistic intake rate regime, supported by empirical data, not only makes reproductive hyperallometry more likely to emerge, but does so at more biologically accurate maturity ages. Thus I predict that fish which exhibit this hyperallometry likely come from environments and foraging dimensions that increase intake rate. The results here support recently published data which suggest hyperallometric fecundity scaling, by endorsing snapshot measures of reproductive output with simulation results for instantaneous fecundity rates. This paper not only suggests that higher intake rate scaling may be more justified in these approaches but also highlights the importance of correctly characterising the growth and fitness contribution of different sized individuals to a population. This will be crucial in generating new hypotheses for testing empirical data and will also be vital in creating space for new theory to develop an understanding of the energetic mechanisms behind fecundity rate allocation. Quantifying the effects of these new findings for fish growth models will have profound implications for fisheries management and for growth modelling as a scientific practice in general.

Keywords

Biomass; energetics; productivity; allometry; life history; fisheries

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1 Introduction

1 Organisms must grow by synthesising biomass from consumed resources in order to progress through ontogeny, or
2 stages of life (Hariharan *et al.*, 2016). The rate of biomass production directly influences fitness at the individual
3 level by constraining the speed at which maturity is reached. Beyond the individual, growth has scalable,
4 measurable impacts at multiple ecological levels, by constraining food-web trophic structure and energy transfer
5 efficiency (Barneche *et al.*, 2018a). Biologists have sought to gain a proximate and ultimate understanding
6 ontogenetic growth for over a century. *Why do organisms grow at a specific rate during a specific stage? Why*
7 *do they stop growing? What causes this? Can growth be controlled, and if so, why? What is the optimal size to*
8 *grow to? When is the optimal age to mature?* Answers to these questions require a theoretical understanding
9 of the energetics of growth and how evolution has selected for the patterns we observe given these constraints.

10 Energetic constraints dictate the variety of sizes and, consequently, the fantastic spectrum of niches resident in
11 the biosphere since most key physiological, ecological and life history traits covary with body size (Peters, 1983;
12 Brown & West, 2000; Schmidt-Nielsen & Knut, 1984; Marshall & White, 2019). To quote Bartholomew (1981)
13 “It is only a slight overestimate to say that the most important attribute of an animal, both physiologically and
14 ecologically, is its size”. As such, growth modelling has historically been a popular endeavor in the biological
15 sciences, demanding a knowledge of the mechanisms which shape resource allocation and evolutionary strategy.
16 This prerequisite has attracted theorists, field ecologists and applied scientists, in a joint endeavor to translate
17 growth as a quantifiable, mathematisable and testable idea into a theoretical, predictive framework (Popper,
18 1962; Popper, 1972; Peters, 1983; West, 2011). Geometric scaling laws are especially relevant to this pursuit
19 since many biological traits scale with body size, governed by a power law: $Y = Y_0 M^\beta$, where Y is the trait to
20 be predicted, M is body mass, and Y_0 and β are empirically-derived constants. These laws have been formalised
21 into “allometric” equations. If $\beta = 1$, the scaling is said to be “isometric” with mass, while if $\beta \neq 1$, the scaling
22 allometric with mass, and plots as a curve on linear axes (Brown & West, 2000).

23 Historically, the approaches used to model ontogenetic growth bifurcate into two major branches. Evolutionary
24 Life History Theory, which relates growth, phenomenologically, to the optimum timing of fundamental life
25 history events, and Ecological Metabolic Theory, which relates growth, mechanistically, to fundamental cellular
26 and energetic processes which constrain the scope for growth.

27 Evolutionary life history theorists have typically employed optimisation techniques to solve for the age and size
28 values, of given life history events, which maximise fitness, e.g. age-at-maturation. The *modus operandi* is to
29 assume that evolution selects for timing and growth strategies which do this by optimising trade-offs among
30 competing traits (Day & Taylor, 1997; Stearns, 1989; Stearns, 1992). Typically, then, simplifying assumptions
31 are made with regard to energetic mechanisms (Day & Taylor, 1997; Kozłowski & Uchmanski, 1987), which are
32 viewed as the end evolutionary result of selection on body size, an exemplar of a “top-down” approach.

33 Conversely, metabolic theorists utilise laws from thermodynamics and enzyme kinetics as a first-principles,
34 “bottom-up” approach to growth problems, starting with energetics and ending with body size (Brown *et al.*,
35 2004). Paradigmatically, lifetime growth is governed by the distribution and transformation of available energy.
36 These bioenergetic growth models are predicated on the premise that growth is constrained by an energy scope
37 or profit. An organism garners energy from its environment at a certain intake rate (revenue), some of which
38 it expends on internal maintenance (metabolism) at a certain rate (cost). Any surplus energy remaining after
39 this expenditure, can then be used to synthesise new biomass for growth (Holdway & Beamish, 1984; Rochet,
40 2001; Enberg *et al.*, 2012; Gemert, 2019). Growth slows because maintenance rate scales with mass to a larger
41 exponent than intake rate (different power laws), so this energy profit decreases with size (see Fig. 1). Extant
42 models generally agree upon a mass exponent of 1 for maintenance rate (double the body mass = double the
43 number of cells), whereas the mass exponent of intake rate has been debated through time, given its derivation
44 from different physiological geometries. Early models suggested a value of 2/3 (Pütter, 1920; Bertalanffy, 1938;

45 Bertalanffy, 1957), due to intake being governed by absorption across a membrane surface (rearrangement of
 46 πr^2). However, recent models tend to use a value of 3/4, proposed by West *et al.* (1997), instead due to energy
 47 transport begin governed by a fractal-like supply network (e.g. capillaries), the result being their “general
 48 ontogenetic growth model”.

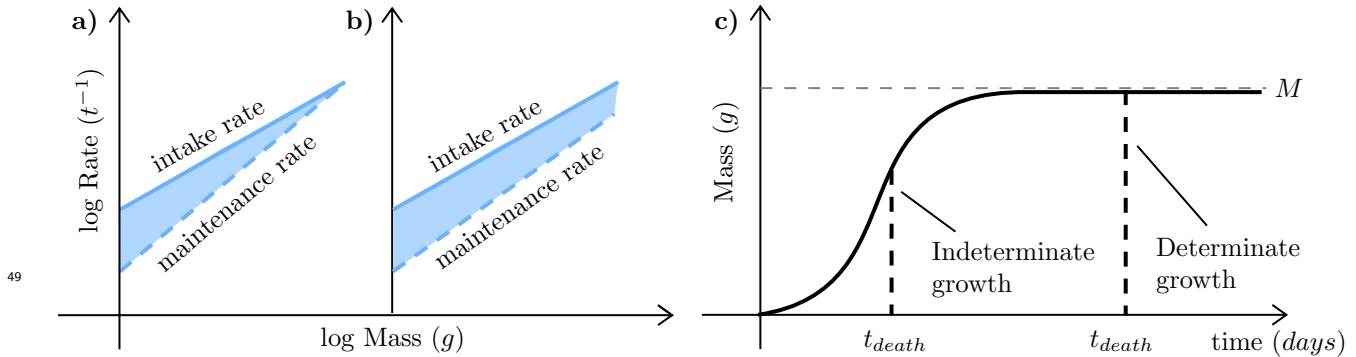


Figure 1: a) Determinate growers reach an asymptotic size when their intake and maintenance rates intersect, which occurs before death, whereas for indeterminate growers, these lines do not intersect before death. NB: after logarithmic transformation of a power law, the slope equals the exponent $\log(am^y) = y \cdot \log(am)$. a) and b) adapted from Marshall & White (2019), c) adapted from West *et al.* (2001) SI.

50 Charnov *et al.* (2001) continued this energetics approach in a fish life history theory framework by developing
 51 the West *et al.* (2001) model to include a fecundity rate term, acknowledging that this only appears at maturity.
 52 Fish are ideal model organisms for growth modelling given their immense ecological and economic importance.
 53 Across a global range of freshwater and marine habitats, they represent the highest vertebrate species richness
 54 and exceed 8 orders of magnitude in their range of body masses (Barneche & Allen, 2018). In fisheries
 55 management, knowledge of time and food required to reach maturity is integral to sustainable management
 56 of stocks (Szwalski *et al.*, 2017; Barneche & Allen, 2018). While Charnov *et al.* (2001), like many previous
 57 studies (see Supplementary Information (SI) Table 2), assumed that fecundity rate scales isometrically with
 58 mass, recently, Barneche *et al.* (2018b) showed that fish reproductive output scales hyperallometrically with
 59 body mass, i.e. larger mothers are disproportionately more fecund. This raises the question of whether the
 60 instantaneous rate of allocation to fecundity, as a continuous process, also scales with mass in this way. As
 61 such, a consequent review extended the Charnov *et al.* (2001) model to include this hyperallometry (Marshall
 62 & White, 2019) (see SI 1.3 for full derivation). However, the data presented by Barneche *et al.* (2018b) render
 63 this model problematic as they represent batch fecundity at discrete time points, a consequence of the typical
 64 sampling technique used to measure fecundity, which involves catch and dissection to take gonad measurements
 65 (Barneche, 2019, pers comm). Unlike intake rate and maintenance rate, this fecundity output term does not
 66 represent an instantaneous rate. Instead it captures snapshots of fecundity at different sizes and it remains
 67 unclear whether this hyperallometry would also emerge for instantaneous rate of allocation. Should this rate
 68 scale hyperallometrically, how fish increase their energy surplus to permit this extra cost comes into question.
 69 Resource intake rate scaling has previously been shown to exhibit environment and dimensionality-dependence,
 70 which most extant models ignore (Pawar *et al.*, 2012). Many assume a simple relationship between energy
 71 intake rate and resting metabolic rate, such that per-capita intake rate scales with consumer body size (m) to
 72 an exponent of 3/4 (see above), irrespective of taxon or environment (Pawar *et al.*, 2012). Environment and
 73 dimension-dependence means that consumption rate can, in fact, scale to an exponent as large as 1.06 and as
 74 low as 0.85, the latter being the approximate mass-scaling exponent of field, or active, metabolic rate (Peters,
 75 1983; Weibel *et al.*, 2004; Pawar *et al.*, 2012). Since foraging, consumption and digestion are active metabolic
 76 processes, it may, in fact, be more prudent to assume a relationship between intake rate and field metabolic
 77 rate, rather than resting (Boisclair & Sirois, 1993). It logically follows that the steeper scaling of intake rate
 78 may provide the energetic scope required for a hyperallometric fecundity rate scaling.

79 Together, these new results on fecundity rate and intake rate scaling reveal disconnects in the ontogenetic growth
80 modelling literature. In this paper, I show that allocation to fecundity, as an instantaneous rate, is theoretically
81 unlikely to exhibit hyperallometric mass-scaling in fish mothers, under the traditional intake rate scaling regime
82 which uses the canonical $3/4$ exponent. By increasing this exponent, causing intake rate to scale steeper with
83 mass, I then show that reproductive hyperallometry is more likely to emerge, due to the compensation effect of
84 the larger intake rate.

85 2 Materials and Methods

To test whether hyperallometry is biologically feasible for an instantaneous rate of fecundity allocation, I developed the Charnov *et al.* (2001) approach by using a biphasic, hybrid model, based on Ecological Metabolic Theory and Life History Theory, which captures the energetics of growth during two distinct ontogenetic stages. Mature fish experience continuous diversion of resources to fecundity which scales to the ρ exponent of mass (see Fig. 2). I also used an updated value of the intake rate coefficient, a , derived from fish-specific energetic values. In order to theoretically endorse their model-fit results for the value of a , West *et al.* (2001) used fundamental cellular properties to derive an approximate value of a . Investigation into this calculation revealed it was flawed when applied to fish data, warranting update (see SI 1.2). The model is as follows:

$$\frac{dm}{dt} = am^{3/4} - bm \quad m < m_\alpha \quad (1)$$

$$\frac{dm}{dt} = am^{3/4} - bm - cm^\rho \quad m \geq m_\alpha \quad (2)$$

86 where $am^{3/4}$ represents hypoallometric intake rate, bm represents isometrically maintenance rate, cm^ρ represents
 87 allometric fecundity rate and m_α is the size at maturity. The model is based on the Life History Theory concept
 88 that natural selection optimises strategies, e.g. c and ρ , to maximise fitness, where lifetime reproductive output
 89 can be used as a proxy for fitness, denoted R_0 , which can be derived from theoretical evolution studies (Charnov
 90 *et al.*, 2001; Stearns, 1992). To this end, I tested the model via simulations which allowed the fecundity rate
 91 parameters c and ρ to vary in order to maximise R_0 , which is calculated using a life history model, developed
 92 from Charnov *et al.* (2001).

93 At any time t , b_t is the *effective* energy allocated by fish to reproduction, the product of the physiological
 94 allocation of resources cm^ρ and an efficiency term h_t representing a declining efficiency of this allocation, known
 95 as reproductive senescence, the natural decline in fecundity as fish age (Stearns, 2000; Benoît *et al.*, 2018; Vrtílek
 96 *et al.*, 2018). This decline begins at maturity (α) and is controlled by a variable rate parameter κ . Fish also
 97 experience an extrinsic mortality rate, or actuarial senescence, contained in a survivorship function, l_t , which is
 98 effectively a declining $\mathbb{P}(\text{survival to } t)$ (Beverton & Holt, 1959; Peterson & Wroblewski, 1984; Charnov, 1993;
 99 Walters & Francis, 1993; Charnov *et al.*, 2001; Benoît *et al.*, 2018; Laird & Sherratt, 2010; Reznick *et al.*, 2002;
 100 Reznick *et al.*, 2006). To the best of my knowledge, this study is the first instance of this incorporation of
 101 reproductive senescence into a growth and life history model. It is important to note than reproductive and
 102 actuarial senescence are functions of time or age, whilst allocation to reproduction is a function of mass. The
 103 instantaneous reproductive output at time t is the product $l_t b_t$ and, thus, the lifetime (cumulative) reproductive
 104 output is represented by the “characteristic equation” (Roff, 1992; Roff, 2002; Stearns, 1992; Arendt, 2011;
 105 Tsoukali *et al.*, 2016):

$$R_0 = \int_{\alpha}^{\infty} cm^\rho h_t l_t dt \quad (3)$$

106 Since fish live in a juvenile and adult phase, they are subject to varying mortality rates across ontogeny (Charnov
 107 *et al.*, 2001). Juvenile mortality ($t_0 \rightarrow t_\alpha$) controls how many fish are alive at α and recruited into the adult
 108 phase. Since this follows an exponential distribution, $l_t = e^{-Z(t)}$ bounded [0,1], it acts as a scaling factor, denoted
 109 l_α , for the mature population ($t_\alpha \rightarrow t_\infty$), which controls how many individuals reach maturity (Charnov, 1990).
 110 For adults, survival is relative to when maturity is reached, $l_t = e^{-Z(t-\alpha)}$. Therefore the lifetime survivorship
 111 of fish is the product of the juvenile survivorship l_α , and adult survivorship:

$$R_0 = c \int_0^{\alpha} e^{-Z(t)} dt \int_{\alpha}^{\infty} m(t)^\rho e^{-(\kappa+Z)(t-\alpha)} dt \quad (4)$$

112 Common in comparative life histories in fish is the use of invariant dimensionless quantities derived from the

113 timing of life history events. That is, across species but within a taxon, certain life history variables, representing
 114 the timing and magnitude of reproduction form dimensionless, invariant ratios (Charnov & Berrigan, 1990;
 115 Charnov, 1993; Prince *et al.*, 2015). It has been shown for fish that the ratio of age-at-maturity and mortality
 116 rate, $\alpha \cdot Z \approx 2$ (Charnov, 1993). Logically, this invariant makes sense since delaying maturation, or increasing
 117 α ($\approx 2/Z$) is only a feasible strategy if the risk of dying is low enough. This is a traditional idea in life history
 118 theory that gaining in one life history trait that increases fitness, e.g. fecundity, is offset by a decline in fitness in
 119 another trait (Charlesworth, 1980; Stearns, 1992; Roff *et al.*, 2006). Rearranging this for Z estimates mortality
 120 rate for a given α value $Z = 2/\alpha$. See SI 2.2 for full derivation of Eq. (4).

121 Maximising R_0 requires analytically solving Eq. (4) for values of c and ρ . Since Eq. (4) has no closed-form
 122 solution, I simulated this numerically using the `DifferentialEquations` and `DiffEqCallbacks` packages in
 123 Julia v1.1.1 (Bezanson *et al.*, 2017), which ran the Rosenbrock optimisation function (Rosenbrock, 1960). The
 124 following parameter space was simulated: $0.001 < c < 0.4$ (Roff, 1983; Enberg *et al.*, 2008; Atiqullah Khan
 125 *et al.*, 2013) and $0.001 < \rho < 1.25$ over a lifespan of $1e6$ days, to ensure all growth trajectory simulations reached
 126 asymptotic size (see Table 1 for full parameterisation). I produced a heat map of the fecundity rate parameter
 127 space, with an optimum c, ρ combination, for a fixed intake rate mass-scaling and reproductive senescence
 128 rate (κ). Since the evolutionary goal is to maximise lifetime reproductive output, natural selection in fish will
 129 inevitably tend towards these optima across time, and thus optimum value combinations theoretically estimate
 if hyperallometrically scaled fecundity rate is possible and likely. *Gonadosomatic Index estimates c ; proportion

Table 1: Notation and parameterisations for the scaling relationships underlying the growth model.

Description		Symbol	Value	Units	Range	Source
Body mass		m		g		
Energy Intake	COEFF	a	2.15	$g \cdot day^{-1}$		West <i>et al.</i> (2001) [†]
Rate	EXP	y	0.75		0.75 - 0.85	Pawar <i>et al.</i> (2012)
Maintenance	COEFF	b	$a/(M)^{0.25}$	$g \cdot day^{-1}$		West <i>et al.</i> (2001)
Rate	EXP	z	1.00			
Fecundity	COEFF	c	VARIABLE	$g \cdot day^{-1}$	0.001 - 0.4	Charnov <i>et al.</i> (2001)
Rate*	EXP	ρ	VARIABLE		0.001 - 1.25	Barneche <i>et al.</i> (2018b)
Age at maturity		α	$2/Z$	day	100 - 400	
Mass at maturity		m_α		g		
Asymptotic/terminal size		M	10000	g		
Probability of survival to time t		l_t				
Rate of instantaneous mortality		Z	$2/\alpha$			

130 of somatic body mass given to repro per year

131 [†]method of derivation from West *et al.* (2001), data from Cummins & Wuycheck (1971) and Steimle & Russell
 132 (1980).

134 2.1 Can instantaneous fecundity rate scale hyperallometrically with mass in fish mothers?

135 Preliminary simulations of the model resulted in some growth curves which exhibit shrinking (i.e. loss of mass
 136 at maturity), due to large values of c and ρ causing too much loss, resulting in $dm/dt < 0$. Since shedding
 137 of somatic mass to reproduce is not biologically realistic, I first screened for these shrinking curves by only
 138 preserving the feasible parameter space of c and ρ which did not cause shrinking. By considering fecundity
 139 allocation as a rate across the entire mature lifetime, which accounts for time in between fecundity output
 140 measurements, I expect hyperallometry to be unlikely, due to the heavy continuous cost this places on fish,
 141 especially when combined with maintenance costs.

142 2.2 Is fecundity rate hyperallometry more likely when intake rate mass-scaling is steeper?

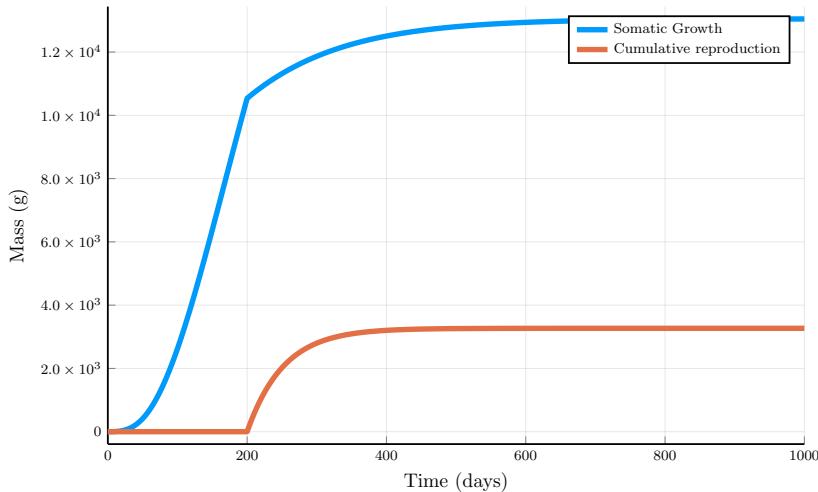
143 The 3/4 scaling of intake rate is set by resting metabolic rate, which scales to the 3/4 exponent of mass (Kleiber,
144 1947; Peters, 1983; Niklas, 1994) due to the approximate fractal architecture of supply networks which become
145 more deeply nested with branches as body size increases (West *et al.*, 1997). This geometry has evolved due
146 to natural selection optimising energy transport to the cells and consequently, as size increases, the number of
147 terminal units (capillaries) scales to the 3/4 exponent of mass (West *et al.*, 1997; West & Brown, 2005). As
148 fractals are mathematically considered to have non-integer dimensions (Hausdorff, 1918; Mandelbrot, 1982),
149 this gives rise to non-integer size-scaling.

150 Resource consumption rate has been shown to scale with mass more steeply than the canonical 3/4 exponent,
151 argued to be more likely related to field metabolic rate mass-scaling (exponent = 0.85), versus resting metabolic
152 rate. Given the restrictive assumptions underlying resting metabolic rate data of no foraging (food is provided
153 *ad libitum*), growth or reproduction, it seems far more prudent to relate intake rate to the mass-scaling of field
154 metabolic rate. This is especially so for the last two assumptions, no growth or reproduction, which are both
155 violated as part of this exercise. Shrinking curves are caused by an inability of intake rate to compensate for
156 the large costs incurred by maintenance rate and high values of c and ρ . Therefore, I predict that increasing
157 the scaling of intake rate to a more biologically realistic value (0.85) will open up the parameter space for larger
158 values of c and ρ , since fish will have more available energy to use, and make fecundity rate hyperallometry
159 more likely.

160 3 Results and Discussion

161 3.1 Can instantaneous fecundity rate scale hyperallometrically with mass in fish mothers?

162 The life history optimisation results show that, theoretically, instantaneous fecundity rate in mature fish is
 163 possible, but unlikely to scale hyperallometrically with mass, under traditional intake rate assumptions. These
 164 results highlight the importance of age-at-maturity in a fish's ability to then devote a large amount of body
 165 mass to reproduction, under the paradigm of the model. In order for fecundity rate to scale hyperallometrically,
 166 results suggest that a fish must mature very early on in its lifetime (see Fig. 5). Immature fish are not subject to
 167 a fecundity rate cost in the model, only maintenance cost (see Eq. (1)), thus they grow far more rapidly than in
 168 the later mature phase (see Fig. 2 inflection) when this extra cost is incurred. Delayed maturity means fish are
 169 free from this cost for longer and thus reach a much larger m_α , which permits only small c and ρ values to avoid
 170 shrinking and maintain physiological feasibility. At maturity, this sudden, overall cost quickly exceeds their
 171 energy intake, especially due to the dominating exponent, causing $dm/dt < 0$, or shrinking, which is stripped
 172 from the feasible parameter space. Therefore, as α , and hence m_α , increases, the optimum ρ decreases (see
 173 Fig. 5). Additionally, sub-optimal values of ρ can exceed the optimum, but this would mandate an exceptionally
 174 low c , as a trade-off, which together do not maximise R_0 (see Fig. 3).



175 **Figure 2:** Growth undergoes an inflection at maturity age $\alpha = 200$, representing the diversion
 of resources to fecundity, leaving less scope for growth.

176 Given that, empirically, fish have been observed to mature after years of growth (in the order of thousands
 177 of days) (Cod: 2-4 years, O'Brien *et al.* (1993), Rochet (2001), and Knickle & Rose (2013); Chinook Salmon:
 178 2-5 years, Groot *et al.* (1991), Yellowtail flounder: 2-5 years, O'Brien *et al.* (1993)), under 3/4 intake rate
 179 scaling, fecundity rate hyperallometry is theoretically unlikely, since such a late α and large m_α would cause
 180 huge fecundity costs and shrinking. In this case, results support previous suggestions that larger adults may
 181 invest relatively less in reproduction, where $0.5 < \rho < 0.9$ (Reiss, 1985; Stearns, 2000). Under a fixed canonical
 182 3/4 intake rate allometry, the only means by which a fecundity rate hyperallometry is theoretically possible is
 183 if fish mature very early in their lifetime, at very small sizes (see Fig. 5), which do not align with empirical
 184 observations. This corroborates the idea that, relative to the timescale of a fish's lifetime, the sexually immature
 185 phase is negligible, and growth is well approximated by a single equation (West *et al.*, 2001). This suggests
 186 that fish effectively experience the costs incurred by sexual maturity (Eq. (2)) from very early on in their
 187 lifetime (West *et al.*, 2001), meaning that this juvenile period of rapid growth, constraining fecundity to scale
 188 hypoallometrically, is, in fact, negligible. If this notion of a negligible, relative juvenile stage holds and fish
 189 do effectively spend all their life being mature, it may then be possible for a fecundity rate hyperallometry to
 190 emerge, although this is still unlikely under 3/4 intake scaling (Fig. 5).

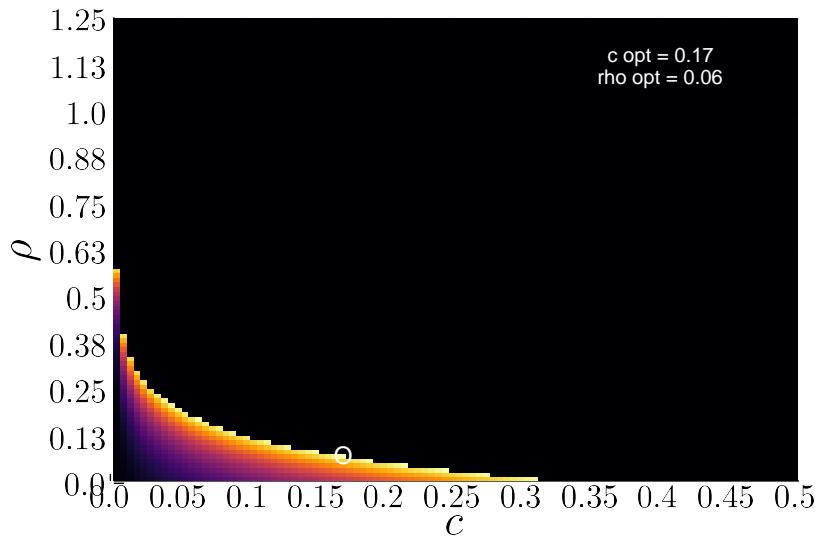
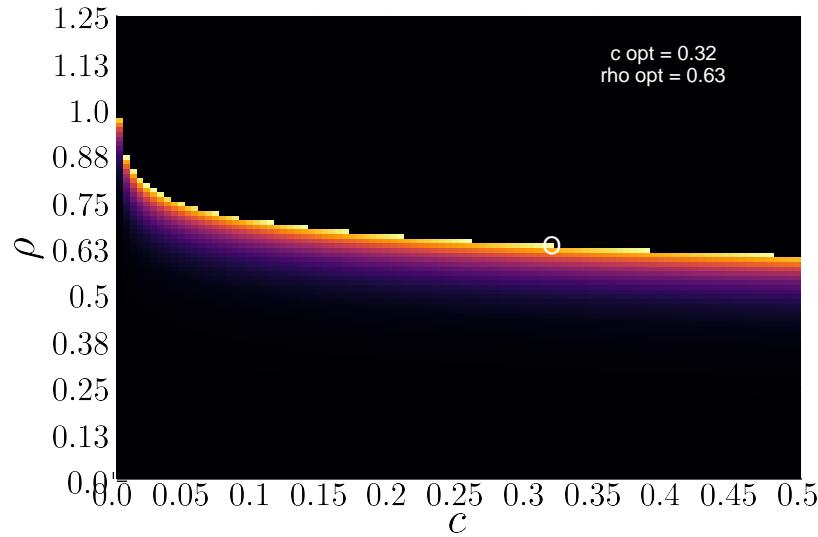


Figure 3: Optimum fecundity rate parameters ρ, c when intake rate $am^x = (2.15)m^{0.75}$, $\kappa = 0.01$. White circle locates optimum combination.

These results highlight the mathematical dynamics of the model which play out given the non-linearity of the intake and fecundity rate terms. Exponents dominate coefficients, so as a result have far narrower ranges of feasible values, evidenced by the shape of the feasible parameter space in Fig. 3. Since I filtered out values which caused shrinking fish, in maintaining biological realism, nearly all scaling exponent values which remained were hypoallometric, except for unrealistically young maturity age and small size (see Fig. 5). By maturing very early, fish effectively do not “let” themselves grow too large, which avoids shrinking.

3.2 Is fecundity rate hyperallometry more likely when intake rate mass-scaling is steeper?

Increasing the value of the intake rate scaling exponent to 0.85 theoretically makes fecundity rate hyperallometry more likely. Steeper intake rate scaling translates the curved fecundity rate parameter space upwards in the ρ plane (Fig. 4 vs Fig. 3), pushing several optimum ρ values above 1 (see Fig. 6). Furthermore, this translation allows for higher fecundity at delayed α , which aligns with my previous claim that 3/4 intake rate scaling constrains fecundity rate scaling to be hypoallometric, given realistic maturity ages (see Fig. 6). Since fish typically mature after years of growth, it logically follows that if fecundity rate hyperallometry exists in nature, intake rate must scale steeper than 3/4. The energy scope required to compensate for the huge fecundity costs at these older α and larger m_α can only originate from here. In essence, under a higher intake regime, fish can delay maturity and reproductive hyperallometry can still emerge at these large m_α sizes due to the larger energy scope provided by steeper scaling. Mathematically, a small alteration to an exponent like this can substantially alter the behaviour of such a model, given that when $m > 1g$, the exponent will dominate any changes in the coefficient. As such, even slight increases in intake rate scaling will permit greater values of c and ρ .



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Figure 4: Optimum fecundity rate parameters ρ, c when intake rate $am^x = (2.15)m^{0.85}$, $\kappa = 0.01$. White circle locates optimum combination.

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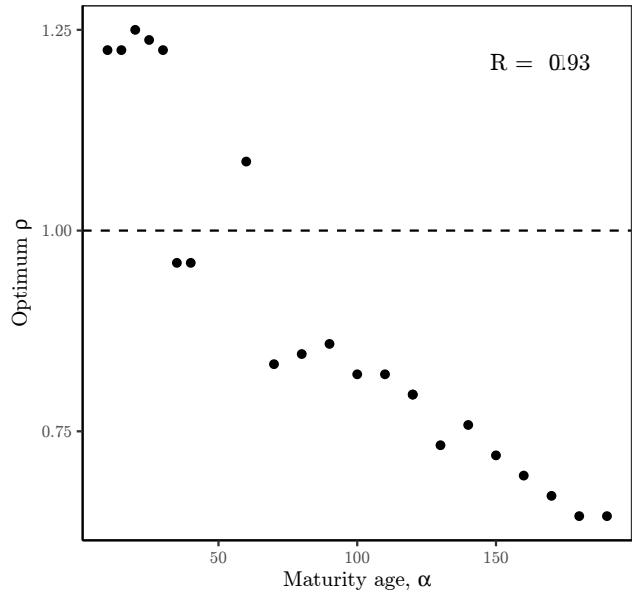
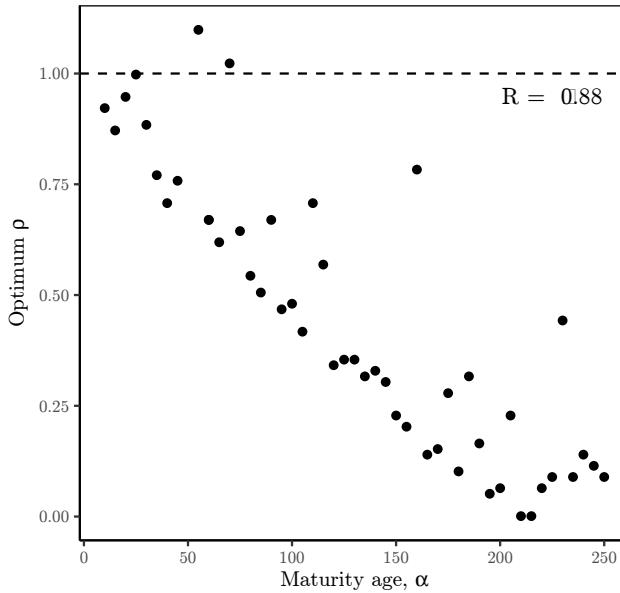


Figure 5: Results of sensitivity analysis of optimum ρ values to α when $am^x = (2.15)m^{0.75}$

Figure 6: Results of sensitivity analysis of optimum ρ values to α for when $am^x = (2.15)m^{0.85}$

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These results extend a dilemma known formerly as “the general life history problem”, in which indeterminate growers, including fish, are subject to a trade-off between increased mortality at maturity and maximising lifetime reproductive output (Roff, 1984; Roff *et al.*, 2006; Stearns, 2000). My results add another layer to this strategy problem, because if a fish can benefit disproportionately in fecundity by delaying maturity and growing larger, permitted by higher intake scaling, life history theory suggests that they should do so, since the evolutionary goal is to maximise R_0 . However, this gain in one trait is countered by an extrinsic mortality rate which lowers their probability of surviving this delay. In a game theoretic sense, the disproportionate gain in fecundity from being larger, resulting from delayed maturity, must be greater than the cost of somatic growth and risk of mortality, in order to be a stable strategy (Arendt, 2011; Enberg *et al.*, 2012). This is already captured by the αZ invariant, since Z has to decrease to allow a greater α , ($\alpha \approx 2/Z$), however *why* a fish would delay maturity is not conveyed by this. One would intuitively think that large body size is selected for, since this has been shown to increase fecundity, improve competitiveness, reduce vulnerability to predators and provide disproportionate access to food in resource-trapped environments (Roff, 2002; Oddie, 2000; French & Smith, 2005; Bashey, 2008; Magnhagen & Heibo, 2001; Craig *et al.*, 2006; Arendt, 2011; Pawar *et al.*, 2012). However, delaying maturity to reach these larger sizes and reap these benefits is only possible if you are likely enough to

survive that long. This concept is well-supported by empirical data that show fish stocks mature earlier under intensive fishing as the probability of survival is so low that their life history evolves in response to maximise R_0 (Rowell, 1993; Rochet, 2001; Swain, 2011). Thus, a trade-off forms where evolution selects for as large a size and late maturity as possible, without increasing risk of death. Simultaneously, growing as rapidly as possible at a young age is of obvious benefit to reduce your chances of predation. Since growing rapidly means investing in growth rather than fecundity, we return to the point that higher intake rate scaling must exist in order to allow this delayed maturity to occur. In fact, it has previously been shown that intraspecific growth rates scale steeper early in ontogeny (Barneche & Allen, 2018), like metabolic rate. This finding actually necessitates steeper intake rate scaling to avoid shrinking at maturity, since this steeper scaling of growth rate would, again, lead to a larger m_α . In fact, in their derivation of 3/4 resting metabolic rate scaling, West *et al.* (1997) even predict that positive deviation from 3/4 intake rate scaling may occur in very small organisms, due to the very short branching of their supply network (Barneche & Allen, 2018). This highlights the multi-dimensionality of an evolutionary life history and game theory approach to understanding and modelling growth.

3.3 Future Direction

Firstly, the results of this study raise questions surrounding our theoretical knowledge of intake rate, since it makes reproductive hyperallometry theoretically more likely. At present we lack substantial empirical data on the duration and frequency of fish foraging bouts, which would improve the accuracy of energy intake parameterisation, and consequently ontogenetic growth models. I expect that, like many biological rates, foraging bout length would scale with body mass ($t = t_0 m^\psi$), related, again, in some way to active metabolic rate. Furthermore, the amount or scaling of consumed biomass itself is not equal to the free energy made available to cells, since the digestion process is inherently subject to some inefficiency (Gemert, 2019). While data on digestion rate scaling is available, empirical data on this efficiency is lacking, especially for fish. Data of this sort could substantially improve our understanding of energy intake in ontogenetic growth models. Potentially, it may be that our understanding of indeterminate growth as a continuous process, is not biologically realistic. Instead, following a glut of resource, animals may pause reproductive efforts in order to maximally grow (Kozlowski & Uchmanski, 1987)

Secondly, this study also highlights the need for an improved theoretical understanding of allocation to fecundity as a rate, and access to empirical data on this for accurate parameterisation. While there may still be area for improvement in our understanding of intake rate, a solid theoretical framework to do so, based on bioenergetics, exists. In light of my results, and the Barneche *et al.* (2018b) and Marshall & White (2019) papers, we now need more empirical data on instantaneous allocation rate to fecundity to improve the our understanding of how fish grow and to develop a first-principles, bioenergetic derivation of this rate. However, collecting empirical data of this form to parameterise such a term will be extremely difficult, given its instantaneous nature.

3.4 Caveats

Several caveats must be acknowledged. First, it is with regret that I could not simulate my model at even higher intake rates, since the likelihood of fecundity rate hyperallometry emerging is evidently contingent on this. Unfortunately, due to computational limitations, iterating through fecundity parameter space in search of optima was not possible at intake rate scaling > 0.85 . Given that consumption rate has been shown to scale to an exponent as high as 1.06, (Pawar *et al.*, 2012), I hope to be able to do this in the future.

Secondly, the maintenance rate parameter b will also have affected the results of my analysis. b is energetically derived from the metabolic rate of a single cell, B_c (see SI 1.1), however this is not independently known (West *et al.*, 2001), and in my model is parameterised for a given fish by rearranging the formula for calculating asymptotic size, $b = a/M^{1/4}$. The caveat here lies in the value for M , which I chose to be a hypothetical value of 20kg, which is in the approximate region of the terminal size of Atlantic cod (*Gadus morhua*). However the

size of this value in the denominator of the equation for b , will of course have consequences for the costs borne by a fish, as a larger asymptotic size will increase this. In reality if this maintenance cost is lower, this would allow energy scope for fecundity rate hyperallometry to emerge more easily. Extending this work would involve using a range of values for b to investigate the effect of this maintenance cost of reproductive hyperallometry.

Thirdly, the results were insensitive to κ , the rate of fecundity decline with age. Perhaps the values I used were unrealistic, given this result. However, parameterisation is extremely difficult since data on reproductive senescence are lacking, due to the difficult of obtaining them, since fish at this age are extremely likely to die. In future work I would attempt to use an effective value of κ to observe the life history consequences, which I predict would be a lower α , since a high κ would make delaying maturity sub-optimal.

Lastly, a possible weakness in the model framework itself is the sudden introduction of a fecundity rate term at α . Of course, fish do not become mature in the timescale of a single day, as in the model, so the “sudden” diversion of resources to reproduction would be far more gradual in real life. However, mathematically, the equilibrium point at asymptotic size would still remain the same under a more progressive onset of reproduction. West *et al.* (2001) avoid this issue by acknowledging the negligible duration of the juvenile stage, using only the mature equation for lifetime growth. Alternatively, while the juvenile phase may not be negligible, it may be that fish allocate resources to reproduction from an early age, such as preparing reproductive organs and developing immunity, termed “dissipative” processes (Kooijman, 2010; Kearney, 2012). This also sheds light on the distinction required in future work, between age-at-maturity and age-at-first-reproduction, since the model assumes that as soon as a fish becomes mature, it immediately commences reproduction. It is also entirely possible that growth is not a continuous process in the fashion I have modelled here. Instead fish may transiently grow during non-reproductive phases (e.g. winter) before investing heavily in reproduction (Kozłowski & Uchmanski, 1987).

3.5 Empirical Predictions

I expect that, given empirical evidence of preferred prey size, combined with my results, intense fishing could drastically decrease the fitness of fish (Brose *et al.*, 1911; Barnes *et al.*, 2010; Gemert, 2019). Since fishing landing gear is designed around catching larger fish, continued intense fishing, as fish as a food base becomes more popular globally, means that we are now selecting for smaller sized fish, by removing their natural predators, the bigger fish. Given the likelihood of steeper intake rate scaling, and hyperallometric fecundity, these smaller fish will likely be disproportionately less fecund, meaning we may be drastically reducing their fitness via reduced R_0 and their reproductive contribution to the population.

Additionally, given more time, I would have aimed to effectively reverse-engineer intake rate scaling of certain fish species, based on their fecundity rate scaling, by cross-referencing the results of Pawar *et al.* (2012) and Barneche *et al.* (2018b). This could potentially reveal whether the outliers in the Barneche *et al.* (2018b), which did not exhibit hyperallometric fecundity scaling ($\approx 5\%$) are known to forage in different environments or dimensions, with lower intake rate scaling. I expect that species showing reproductive hyperallometry would come from these high intake habitats, since theory suggests they should maximise R_0 if the energy scope allows.

308 **4 Conclusion**

309 In conclusion, my results suggest that, under a steeper allometric scaling of intake rate, fecundity rate is more
310 likely to scale hyperallometrically in maximising lifetime reproductive output. Given existing empirical data
311 on fish maturity age, these findings suggest that this intake rate is more realistic than the traditionally used
312 value, since observed maturity ages and high fecundity would not be theoretically possible without higher intake
313 rate. Several parameters contain gaps, including an accurate first-principles derivation of maintenance cost and
314 empirical data on fish foraging duration, which will both impact the energetic scope for growth. I invite other
315 studies to refute the results reported here and also call for new empirical data to be published on resource
316 consumption in fish to gain a better theoretical understanding of intake rate, which may scale steeper still.

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