

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

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Declaration of Originality

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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.

Contributions: Dr Samraat Pawar, Dr Diego Barneche, Dr Van Savage and Tom Clegg conceived the study. Diego Barneche compiled data on fish growth. S.P., T.C. and L.V. developed the idea.

Luke Joseph Vassor
August 28, 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 an energetics and life history theoretical model to estimate the optimum mass-proportion and mass-scaling values of fecundity rate in fish, under different energy intake regimes, to test a recent claim that it scales hyperallometrically with mass. Theoretically, I show that a truly continuous rate of allocation to fecundity cannot scale hyperallometrically with size. I also derive and validate the use of a new intake rate value, based on fish energetics data and field metabolic rate mass-scaling, by demonstrating that the onset of reproductive allocation at maturity is only possible given these intake rate values. Overall, the study highlights the importance of correctly characterising growth and the fitness contribution of different sized individuals to a population.

Keywords

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

Acknowledgements

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1 Introduction

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

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

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

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

Conversely, metabolic theorists utilise laws from thermodynamics and enzyme kinetics as a first-principles approach to growth problems, starting with energetics and ending with body size, i.e. a “bottom-up” approach (Brown *et al.*, 2004). Paradigmatically, lifetime growth is governed by the distribution and transformation of available energy. These bioenergetic growth models are predicated on the premise that growth is constrained by an energy scope or profit. An organism garners energy from its environment at a certain rate (revenue), some of which it expends on internal maintenance (metabolism) at a certain rate (cost). Any surplus energy remaining after this expenditure, can then be used to synthesise new biomass for growth (Holdway & Beamish, 1984; Rochet, 2001). Growth slows because maintenance rate scales with mass to a larger exponent than intake rate (different power laws), so this energy profit decreases with size (see Section 1). Extant models agree upon a mass exponent of 1 for maintenance rate (double the body mass = double the number of cells), whereas the mass exponent of intake rate has been debated through time, given its derivation from different geometric mechanisms. Early models suggested a value of 2/3 (Pütter, 1920; Bertalanffy, 1938; Bertalanffy, 1957), due to intake being governed by absorption across a membrane surface (rearrangement of πr^2). However, recent models tend to use a value of 3/4, proposed by West *et al.*, (1997), instead due to energy transport being governed by a fractal-like supply network (e.g. capillaries), the result being their “general ontogenetic growth model”:

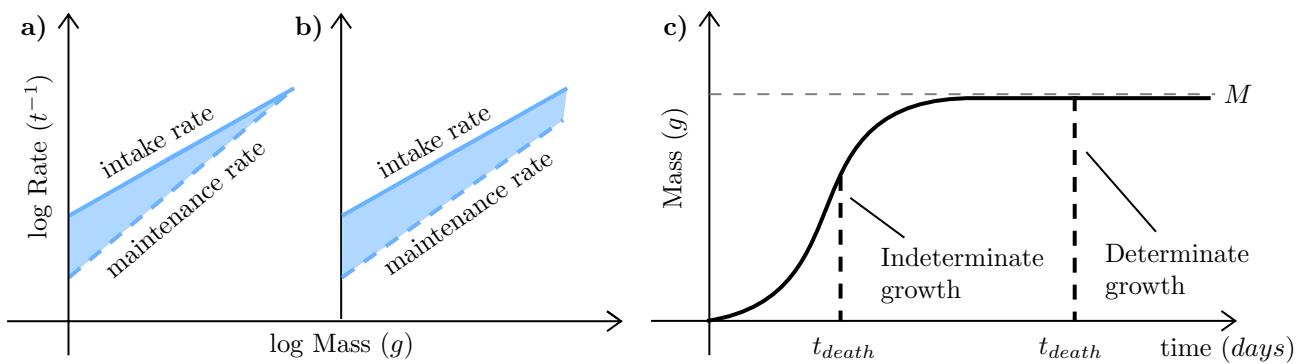


Figure 1: a) Determinate growers reach an asymptotic size when their intake and maintenance rates intersect, which occurs before death whereas for indeterminate growers, these lines do not intersect before death. NB: after logarithmic transformation of a power law, the slope equals the exponent $\log(am^y) = y \cdot \log(am)$.

Charnov *et al.*, (2001) continued this energetics approach in a fish life history framework by developing the West *et al.*, (2001) model to include a fecundity rate term, acknowledging that this only appears at maturity. Fish are ideal model organisms for growth modelling given their immense ecological and economic importance. Across a global range of freshwater and marine habitats, they represent the highest vertebrate species richness and exceed 8 orders of magnitude in their range of body masses (Barneche & Allen, 2018). In fisheries management, knowledge of time and food required to reach maturity is integral to sustainable management of stocks (Szuwalski *et al.*, 2017; Barneche & Allen, 2018). While Charnov *et al.*, (2001) assumed that fecundity rate scales isometrically with mass, recently, Barneche *et al.*, (2018b) showed that fish reproductive output scales hyperallometrically with body mass, i.e. larger mothers are disproportionately more fecund. This opened the question of whether the rate of allocation to fecundity also scales with mass in this way. As such, a consequent review extended the Charnov *et al.*, (2001) model to include this hyperallometry (Marshall & White, 2019) (see SI for full derivation). However the data presented by Barneche *et al.*, (2018b) are problematic as they represent batch fecundity at discrete time points, a consequence of the typical sampling technique used to measure fecundity, which involves catch and dissection to take gonad measurements (Barneche, 2019, pers comm). Unlike intake rate and maintenance rate, this fecundity output term is not based on an instantaneous rate. Instead it captures snapshots of fecundity at different sizes and it remains unclear whether this hyperallometry would apply to an instantaneous rate of allocation across continuous time. Should this rate scale hyperallometrically with mass, how they increase their energy surplus to permit this extra cost comes into question.

Resource intake rate scaling has previously been shown to exhibit environment and dimensionality-dependence, which most extant models ignore (Pawar *et al.*, 2012). Many assume a simple relationship between energy intake rate and resting metabolic rate, such that per-capita resource supply scales with consumer body size (m) to an exponent of 3/4 (see above), irrespective of taxon or environment (Pawar *et al.*, 2012). Environment and dimension-dependence means that consumption rate can, in fact, scale to an exponent as large as 1.06 and as low as 0.85, the latter being the approximate mass-scaling exponent of field metabolic rate (Peters, 1983; Weibel *et al.*, 2004; Pawar *et al.*, 2012). Since fish experience field conditions throughout life, it may, in fact, be more prudent to assume a relationship between intake rate and field metabolic rate, rather than resting (Boisclair & Sirois, 1993). It logically follows that the steeper scaling of intake rate may provide the energetic compensation required for a hyperallometric fecundity rate scaling.

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

These theoretical findings will be crucial in generating new hypotheses for testing empirical data and for highlighting the distinction between continuous rate data and discrete time data. Further, these findings likely warrant update of how existing models consider intake rate, since the reason we do not observe shrinking trajectories in reality may be because larger intake rate scaling permits larger (hyperallometric) scaling exponents of fecundity. They will also be in creating space for new theory to develop in understanding 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.

2 Materials and Methods

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

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 which utilises 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 of their calculation of a revealed it was flawed when applied to fish data, warranting update (see SI).

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

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

The model is based on the Life History Theory concept that natural selection optimises strategies, e.g. c and ρ , to maximise fitness, where lifetime reproductive output can be used as a proxy for fitness, denoted R_0 , which can be derived from theoretical evolution studies (Charnov *et al.*, 2001; Stearns, 1992). To this end, I tested the model via simulations which allowed the fecundity rate parameters c and ρ to vary in order to maximise R_0 , which is calculated using a life history model, developed from Charnov *et al.*, (2001).

At any time t , b_t is the *effective* energy allocated by fish to reproduction, the product of the physiological allocation of resources cm^ρ and an efficiency term $h(m)$ representing a declining efficiency of this allocation, known as reproductive senescence, the natural decline in fecundity as fish age (Stearns, 2000; Benoît *et al.*, 2018; Vrtílek *et al.*, 2018). This decline begins at maturity (α) and is controlled by a variable rate parameter κ . Fish also experience an extrinsic mortality rate, or actuarial senescence, contained in a survivorship function, l_t , which is effectively a declining $\mathbb{P}(\text{survival to } t)$ (Bevertton & Holt, 1959; Peterson & Wroblewski, 1984; Charnov, 1993; Walters & Francis, 1993; Charnov *et al.*, 2001; Benoît *et al.*, 2018; Laird & Sherratt, 2010; Reznick *et al.*, 2002; Reznick *et al.*, 2006). To the best of my knowledge, this study is the first instance of this incorporation of reproductive senescence into a growth and life history model. It is important to note than reproductive and actuarial senescence are functions of time or age, whilst allocation to reproduction is a function of mass. Thus, the instantaneous reproductive output at time t is the product $l_t b_t$ and the lifetime (cumulative) reproductive output is:

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

Since fish live in a juvenile and adult phase, they are subject to varying mortality rates through ontogeny (Charnov *et al.*, 2001). Juvenile mortality ($t_0 \rightarrow t_\alpha$) controls how many fish are alive at α and recruited into the adult phase. Since this follows an exponential distribution, $l_t = e^{-Z(t)}$ bounded [0,1], it acts as a scaling factor, denoted L_α , for the mature population ($t_\alpha \rightarrow t_\infty$), which controls how many individuals reach maturity (Charnov, 1990). For adults survival is relative to when maturity is reached, $l_t = e^{-Z(t-\alpha)}$. Therefore the lifetime survivorship of fish is the product of the juvenile survivorship, L_α and adult survivorship. Together these form the “characteristic equation” (Roff, 1992; Roff, 2002; Stearns, 1992; Arendt, 2011; Tsoukali *et al.*, 2016):

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

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

Maximising R_0 requires analytically solving Eq. (4) for values of c and ρ which do so. Since Eq. (4) has no closed-form solution, I simulated this numerically using the `DifferentialEquations` and `DiffEqCallbacks`

packages in Julia v1.1.1 (Bezanson *et al.*, 2017), which ran the Rosenbrock optimisation function (Rosenbrock, 1960). The following parameter space was simulated: $0.001 < c < 0.4$ (Roff, 1983; Enberg *et al.*, 2008; Atiqullah Khan *et al.*, 2013) and $0.001 < \rho < 1.25$ over a lifespan of $1e6$ days, to ensure all growth trajectory simulations reached asymptotic size. I produced a heatmap of the fecundity rate parameter space, with an optimum c, ρ combination, for a fixed intake rate mass-scaling and reproductive senescence rate (κ). Since the evolutionary goal is to maximise lifetime reproductive output, natural selection in fish will inevitably tend towards these optima across time, and thus optimum value combinations theoretically estimate if hyperallometrically scaled fecundity rate is possible.

Preliminary simulations of the model resulted in some growth curves which exhibit shrinking (i.e. loss of mass at maturity), due to large values of c and ρ causing too much loss, resulting in $dm/dt < 0$. Since shedding of somatic mass to reproduce is not biologically realistic, I first screened for these shrinking curves by only preserving the feasible parameter space of c and ρ which did not cause shrinking. By considering fecundity allocation as a rate across the entire fish lifetime which accounts for time in between fecundity output measurements, I expect the mass-scaling to go down because ..

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

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

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

3 Results and Discussion

Production of a fecundity-rate feasibility heatmap proved necessary to obtain growth curves which did not shrink, but instead experienced an inflection, where growth rate remained positive ($dm/dt > 0$) as energy is diverted to reproduction at age α (see Fig. 2).

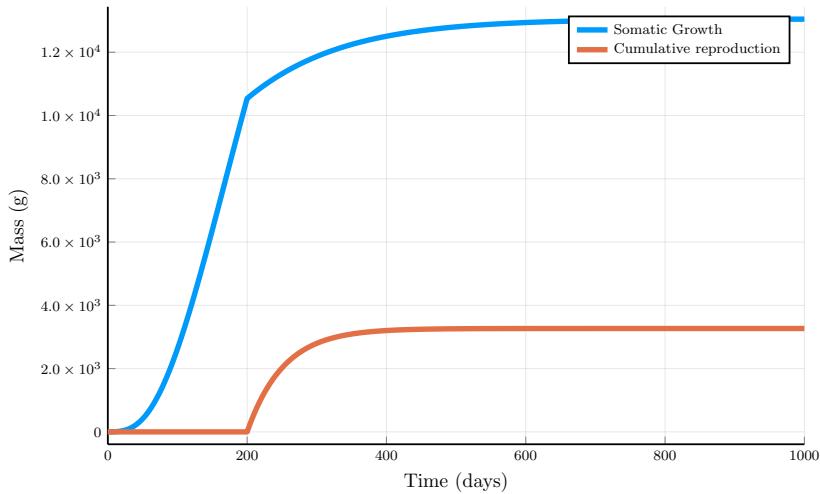


Figure 2: Growth undergoes an inflection, as it approaches an asymptote, at maturity when $\alpha = 200$, as opposed to shrinking, which would be rejected by the optimisation algorithm since shrinking in fish is not biologically possible. At maturity, growth rate slows (inflection) due to the diversion of resource to fecundity, leaving less scope for growth. Simultaneously, lifetime reproduction (cumulative) increases to an asymptote, when this quantity is less and less likely to increase given the exponential decay of survivorship probability, l_t .

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

The life history optimisation results show that, theoretically, instantaneous fecundity rate in mature fish is unlikely to scale hyperallometrically with mass. These results highlight the importance of age-at-maturity in a fish's ability to then devote a large proportion of body mass to reproduction, under the paradigm of the model. In order for fecundity rate to scale hyperallometrically, of which there was a single instance, a fish must mature very early. Immature fish are not subject to a fecundity rate cost in the model, only maintenance cost (see Eq. (1)), thus they grow far more rapidly than in the later mature phase (see Fig. 2) when this extra cost is incurred (see logistic growth). Moreover, if this growth rate is too rapid, fish will reach a size at maturity m_α which is too large (Arendt, 2011) to permit fecundity rate hyperallometry, as an exponent of their large mass, the cost is greater than what is physiologically feasible. At maturity their overall cost quickly exceeds their energy intake, causing $dm/dt < 0$ or shrinking. Therefore, as maturity age increases, the optimum ρ decreases (see Fig. 5). This highlights 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, the only scaling exponent values which remained were hypoallometric, except for the one instance of hyperallometry at a very young maturity age and small size (see Fig. 5). If α is, in reality, in the order of hundreds of days, or years, then fecundity rate hyperallometry is not theoretically possible. In this case, these results support previous suggestions that larger adults invest relatively less in reproduction, with mass-scaling exponents of 0.5 - 0.9 (Reiss, 1985; Stearns, 2000). At these older maturity ages, fish will have reached much larger sizes (given the lack of fecundity cost), and so only small c and ρ values are permitted to avoid shrinking. Under the canonical 3/4 mass-scaling of intake rate, the only way that hyperallometric fecundity rate is theoretically possible is if fish mature very early in their lifetime, at small sizes. These results corroborate this idea since optimum ρ values decrease with maturity age (Fig. 5), potentially supporting the idea that relative to the timescale of a fish's lifetime, the sexually immature phase is negligible, therefore growth is well approximated by a single equation which encompasses the costs incurred by sexual maturity (Eq. (2)) in their lifetime (West *et al.*, 2001). The speed at which fish reach maturity in early life means they can essentially be viewed as being born mature. By maturing very early, fish effectively do not "let" themselves grow too large.

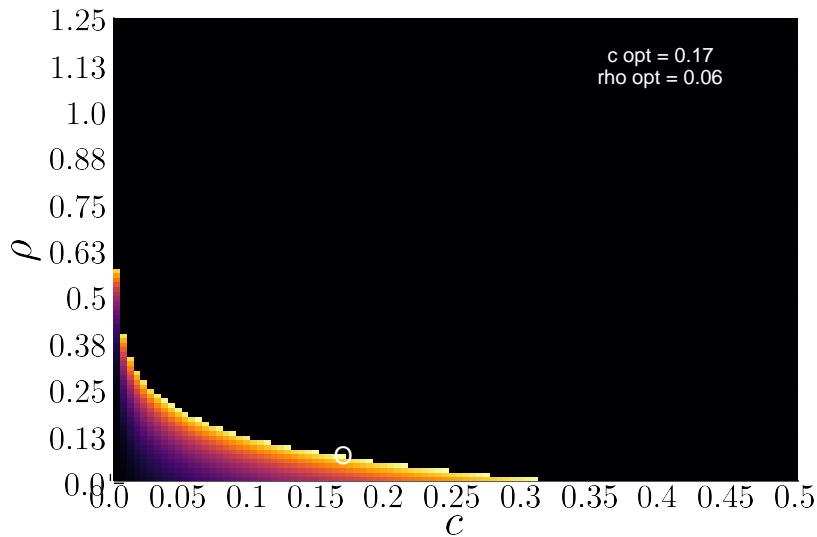


Figure 3: Optimum fecundity rate parameters ρ, c when $am^x = (2.15)m^{0.75}$, $\kappa = 0.01$. White circle locates optimum combination.

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. Furthermore, it endorses the above claim regarding maturity age by permitting hyperallometry at older maturity ages (see Fig. 6). In essence, under a higher intake regime, fish can delay maturity and reproductive hyperallometry can still emerge at these large sizes due to the larger energy scope. Increased intake rate 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). This is an intuitive result, since the steeper scaling of intake rate now provides the energy needed to compensate for the extra loss incurred by higher fecundity rates, which will be optimally increased to maximise lifetime reproduction. 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 .

These results extend a dilemma known formerly as “the general life history problem”, in which indeterminate growers are subject to a trade-off between increased mortality at maturity and maximising lifetime reproductive output (Roff *et al.*, 2006; Stearns, 2000). Given these results, if a fish can benefit disproportionately in fecundity by delaying maturity (which is permitted by higher intake scaling) and growing larger, they face the decision of doing so while simultaneously decreasing their probability of surviving that long. Essentially, the reward in delayed fecundity (resulting from hyperallometry) must be greater than the risk of mortality (Arendt, 2011). Given that, empirically, fish have been observed to mature after years of growth, rather than instantly, (Cod: 2-4 years, O’Brien *et al.*, (1993), Rochet, (2001), and Knickle & Rose, (2013); Chinook Salmon: 2-5 years, Groot *et al.*, (1991), Yellowtail flounder: 2-5 years: O’Brien *et al.*, (1993)), if fecundity rate hyperallometry is true, then we can predict that one of two things must be occurring: either intake rate scales steeper than the canonical 3/4 to allow them to mature that late, or their adult mortality rate is less than expected. The latter is already captured by the αZ invariant, since Z has to decrease to allow a greater α , a broad however this exists under the assumption high mortality rate disincentivises fish from delaying maturity without consideration of the benefits, which include greater fecundity, more competitive and less vulnerable (Arendt, 2011) FORWARD CITE. It may be that even when Z remains high, in a game theoretic sense, it is still optimal to delay maturity to benefit from the hyperallometric fecundity.

These results highlight the multi-dimensionality of an evolutionary life history theory approach to growth. 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). If these advantages were able to more than offset the heavy mortality cost of being disproportionately more fecund at larger sizes, then one would expect that later maturity is always preferable, assuming that energy intake needs are met. However, if they do not offset this mortality cost then a trade-off is born since evolution will select as late a maturity age as possible,

given the mortality rate, which maximises lifetime reproductive output.

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 do not have enough empirical data, regarding the duration and frequency of fish foraging bouts, to make more accurate predictions about their realised energy intake. Furthermore, it is very difficult to integrate the disconnected timescales of these bouts, presumably a timescale of hours, and ontogenetic lifetime, presumably a timescale of years. Given that intake rate is derived from a rate of incoming energy per day, more accurate data on actual energy obtained by a fish throughout the day will allow improved growth modelling. This demands a knowledge of the digestion efficiency of fish, since they cannot utilise every gram of resource they consume, and how the timescale of foraging bout scales with mass, a power law which is yet unknown. Knowledge of this sort could have profound consequences for ontogenetic growth models. For example, 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 (Kozłowski & Uchmanski, 1987)

Secondly this study also highlights the need for an improved theoretical understanding of allocation to fecundity as a rate. While there may still be area for improvement in the derivation of intake rate, a solid theoretical framework, based on bioenergetics, exists. In light of my results, and the Barneche *et al.*, (2018b) and Marshall & White, (2019) papers, we now need a first-principles, bioenergetic derivation of instantaneous allocation rate to fecundity. Given the near impossibility of collecting empirical data of this form in continuous time, SOMETHING/

If anything it is actually necessary to have higher allometry scalings (assuming rho has a physiological maximum) at later maturity ages because they must compensate for the lost time to maximise lifetime repro. Delay wouldn't be a strategy if they couldn't do this (counter argument is that they delay it for the other reason, competition and less vulnerable (Arendt, 2011))

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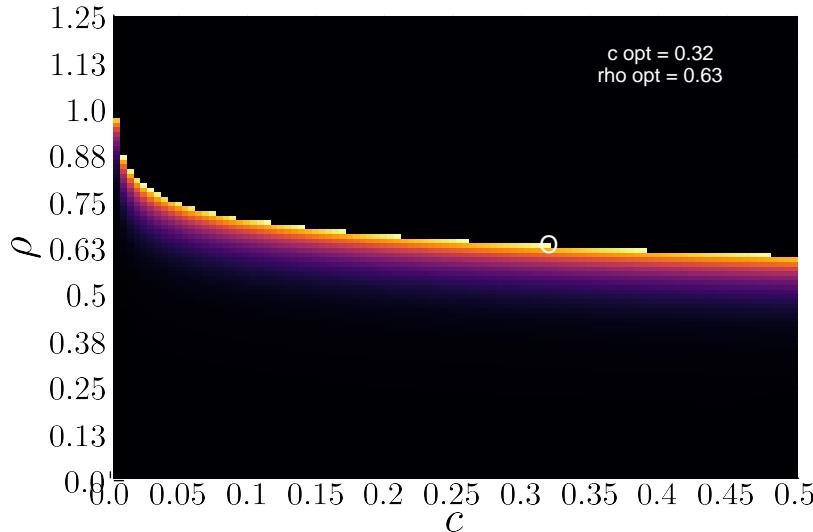


Figure 4: Optimum fecundity rate parameters ρ, c when $am^x = (2.15)m^{0.85}$, $\kappa = 0.01$. White circle locates optimum combination.

Results also appear unaffected by a changing κ , suggesting that the decline in fecundity does not occur at a large enough magnitude to overcome the investment in reproduction itself.

3.3 Caveats

These results highlight a caveat of the model, which is that the fixed parameter α has a fundamental effect on the feasible parameter space. The aforementioned αZ invariant does, of course, cause the life history model (Eq. (4)) to behave the same regardless of the chosen α , since Z compensates. However, this invariant does not discipline the growth model (Eq. (2)), which is where predictive power begins to be lost. The results presented reflect $\alpha = 200$, or a fish maturity age of 200 days. b is also a caveat as this dictates growth size and juvenile ages and calculated from rearrangement of a and M

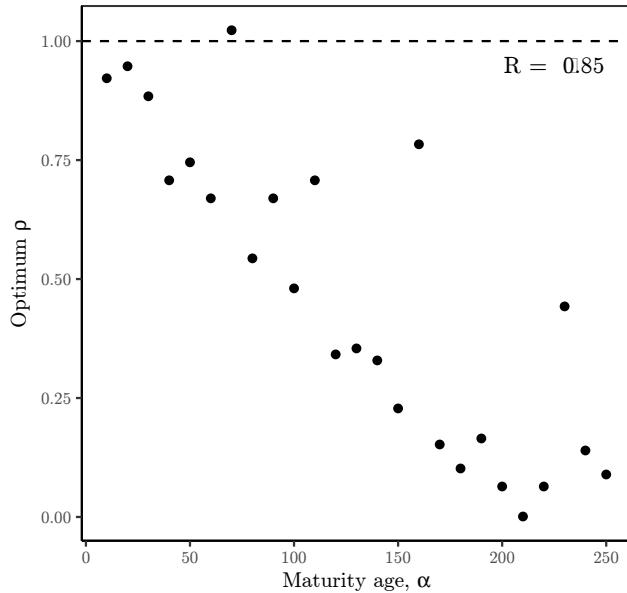


Figure 5: Results of sensitivity analysis of optimum ρ values to α when $am^x = (2.15)m^{0.75}$

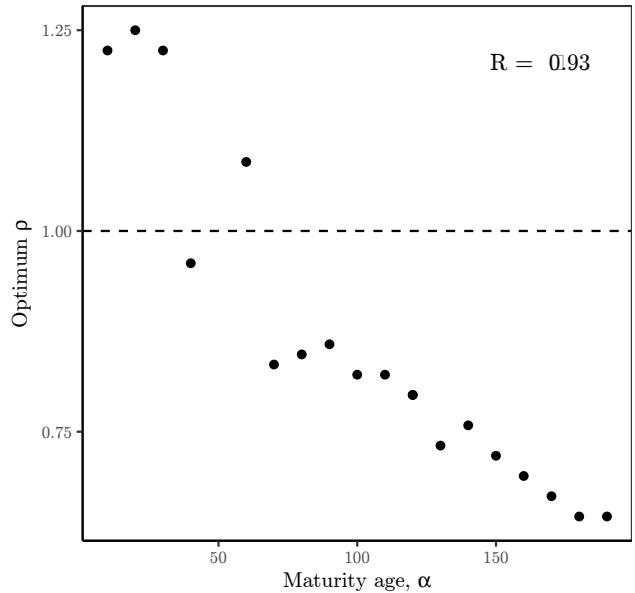


Figure 6: Results of sensitivity analysis of optimum ρ values to α for when $am^x = (2.15)m^{0.85}$

Alternatively, this would indicate that the architecture of the model itself is not realistic, in the sense that fish do not suddenly become mature in the timescale of a single day and incur an immediately large cost. Instead, they either allocate to fecundity from a very early age while remaining sexually immature, termed “the dissipative processes of respiration”

3.4 Empirical Predictions

4 Conclusion

My conclusion.

Produce
more alpha
values for
denser plots

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