

Online Supplement:

Deriving population scaling rules from individual-level metabolism
and life history traits,
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Supplement A: Data collected and statistical analysis

Table S.A1: Summary of the data collected per species group.

Group	Trait	No. species	References
Bivalves	Growth rate A	637	(1)
	Offspring size	49	(2)
Teleosts	Growth rate A	719	(3) (4) (5)
	Offspring size	84	(6) (4)
	Population growth rate	199	(3)
Elasmobranchs	Growth rate A	6	(4)
	Offspring size	25	(6) (4)
	Population growth rate	103	(7)
Copepods	Growth rate A Active feeders	26	(8) (9)
	Growth rate A Passive feeders	4	(8) (9)
	Offspring size	42	(6)
Mammals	Growth rate A	52	(3)
	Offspring size	59	(6)
	Population growth rate	70	(3)

References: (1) Moss et al. (2016); (2) Kooijman (2009); (3) Hutchings et al. (2012); (4) Andersen (2019); (5) (Froese and Pauly, 2018) (6) Neuheimer et al. (2015); (7) Zhou et al. (2012); (8) Kiørboe and Hirst (2014); (9) Serra-Pompei et al. (2020)

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Table S.A2: Statistical analysis of somatic growth rate A and offspring size M_0 with asymptotic weight M_∞ with a and b being the intercepts and slopes of the linear regressions. Bold P-values indicate parameters significantly different from 0 (P-values < 0.05).

Trait	Group	b	P-value b	a	P-value a
somatic growth rate A	Teleost	4.3×10^{-2}	6.5×10^{-5}	3.6	$< 2 \times 10^{-16}$
	Elasmobranch	2.4×10^{-2}	0.70	5.5	5.9×10^{-3}
	Bivalves	0.21	$< 2 \times 10^{-16}$	0.98	1.16×10^{-12}
	Copepods (Active)	0.09	0.06	6.4	$< 2 \times 10^{-16}$
	Copepods (Passive)	0.18	0.09	2.67	1.5×10^{-3}
Offspring size M_0	Teleost	0.092	0.21	6.8×10^{-4}	$< 2 \times 10^{-16}$
	Elasmobranch	1.2	4.2×10^{-8}	9.6×10^{-4}	5.6×10^{-5}
	Bivalves	-0.03	0.40	6.3×10^{-7}	$< 2 \times 10^{-16}$
	Copepods	0.67	$< 2 \times 10^{-16}$	1.3×10^{-3}	$< 2 \times 10^{-16}$
	Mammals	1.1	$< 2 \times 10^{-16}$	0.85	0.26

Supplement B: Solving the McKendric-von Forster equation

Before considering the case of size-structure population, let us consider the population growth rate for a any kind of population. The simplest population model would be a Malthusian model $d\phi(t)/dt = r_{\max}\phi(t)$, where $\phi(t)$ is a given characteristic of the population size (e.g. number, biomass, concentration). The population growth rate r_{\max} , expressed with dimensions 1/time, describes the rate of change of ϕ over time. The Malthusian population model is growing exponentially with time $\phi(t) = \phi_0 e^{r_{\max}t}$. It assumes a population with abundant resource and negligible density dependence. Additional density dependent processes will reduce the population growth rate, so r_{\max} is the maximum population growth rate. Let us now consider a size-structured population, for which we want to solve the number density $\phi(m, t)$. The number density is a solution to the McKendric-von Foerster equation:

$$\frac{\partial \Phi(m, t)}{\partial t} + \frac{\partial g(m)\Phi(m, t)}{\partial m} = -\mu(m)\Phi(m, t), \quad (\text{S.B1})$$

where, $g(m)$ is the growth rate (mass per time) and $\mu(w)$ is the mortality rate (per time), that are both constant over time. Following the Malthusian model, we hypothesise that (S.B1) allows a solution of the form:

$$\Phi(m, t) = v(m)e^{r_{\max}t}, \quad (\text{S.B2})$$

where the number density has two independent parts: $v(m)$ the weight dependent form and the time dependent part $e^{r_{\max}t}$. We first find a solution for $v(m)$ by inserting (S.B2) in (S.B1). Knowing the derivative of $\Phi(m, t)$ ((S.B2)) and the derivative of a product of functions we get that:

$$v(m)r_{\max}e^{r_{\max}t} = -e^{r_{\max}t} \left[\frac{dg(m)}{dm}v(m) + \frac{dv(m)}{dm}g(m) + \mu(m)v(m) \right]$$

By simplifying

$$v(m)r_{\max} = -\frac{dg(m)v(m)}{dm} - \mu(m)v(m).$$

We can rewrite this equation to express $v(m)$ as a differential equation:

$$\frac{dv(m)}{dm} = - \left[\frac{dg(m)}{dm} + r_{\max} + \mu(m) \right] \frac{v(m)}{g(m)}. \quad (\text{S.B3})$$

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For the sake of simplicity we assume that juveniles invest energy only in growth and adults invest the whole energy in reproduction. This representation does not consider that individual can grow after maturation. To compensate we consider that individuals become mature at the asymptotic size rather than the maturation size. The juvenile growth rate is then equal to the available energy $g(m) = Am^n$ and the mortality $\mu(m) = Aam^{n-1}$. Then the previous equation can be rewritten:

$$\frac{dv(m)}{dm} = F(m)v(m),$$

with $F(m) = -\left[(n + \frac{Aa}{A})m^{-1} + \frac{r_{\max}}{Am^n}\right]$. A solution for this equation is found by integrating $F(m)$ from the offspring size M_0 :

$$\begin{aligned} \int_{M_0}^M f(m)dm &= - \int_{M_0}^M \left[(n+a)m^{-1} + \frac{r_{\max}}{Aw^n} \right] dw \\ &= -(n+a) \ln\left(\frac{M}{M_0}\right) - \frac{r_{\max}}{A(1-n)} (M^{1-n} - M_0^{1-n}) \end{aligned}$$

Then the solution for $v(m)$ is

$$v(m) = C \frac{M_0^{-n}}{A} \left(\frac{M}{M_0}\right)^{-(n+a)} \exp\left[-\frac{r_{\max}}{A(1-n)}(m^{1-n} - M_0^{1-n})\right], \quad (\text{S.B4})$$

where C is a constant of integration. To find C we have to consider the boundary condition of the McKendrick-von Foerster equation (S.B1). Assuming that adults invest all energy in reproduction, then number of new offspring is given by the product of available energy for adults $g(M)$ by the mass of adults $N(M)M$, divided by the offspring size M_0 . The production of new offspring is restricted by the reproduction efficiency ϵ_R

$$\Phi(M_0, t) = \epsilon_R g(M) \Phi(M, t) \frac{M}{M_0}.$$

The weight dependent part of $\Phi(M_0, t)$ is:

$$v(M_0) = C = \epsilon_R g(M) v(M) \frac{M}{M_0} \quad (\text{S.B5})$$

$$= \epsilon_R A M^n v(M) \frac{M}{M_0} \quad (\text{S.B6})$$

Inserting (S.B6) in (S.B4), then the weight-dependent part of the solution for adults is

$$v(M) = \epsilon_R M_0^{-n} M^n v(M) \frac{M}{M_0} \left(\frac{M}{M_0}\right)^{-(n+a)} \exp\left[-\frac{r_{\max}}{A(1-n)}(M^{1-n} - M_0^{1-n})\right]$$

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$$\Leftrightarrow \exp \left[\frac{r_{\max}}{A(1-n)} \left(M^{1-n} - M_0^{1-n} \right) \right] = \epsilon_R \epsilon_{\text{eeg}} \left(\frac{M}{M_0} \right)^{1-a}$$

$$\Leftrightarrow \frac{r_{\max}}{A(1-n)} (M^{1-n} - M_0^{1-n}) = (1-a) \ln \left(\frac{M}{M_0} \right) + \ln(\epsilon_R \epsilon_{\text{eeg}})$$

We finally can write a solution for r_{\max} :

$$r_{\max} = \frac{A(1-n)}{(M^{1-n} - M_0^{1-n})} (1-a) \ln \left(\frac{M}{M_0} \right) + \ln(\epsilon_R \epsilon_{\text{eeg}})$$

Assuming that $M \gg M_0$ we can approximate r_{\max} as:

$$r_{\max} \approx A(1-n)M^{n-1} [(1-a) \log(M/M_0) + \log(\epsilon_R)] .$$

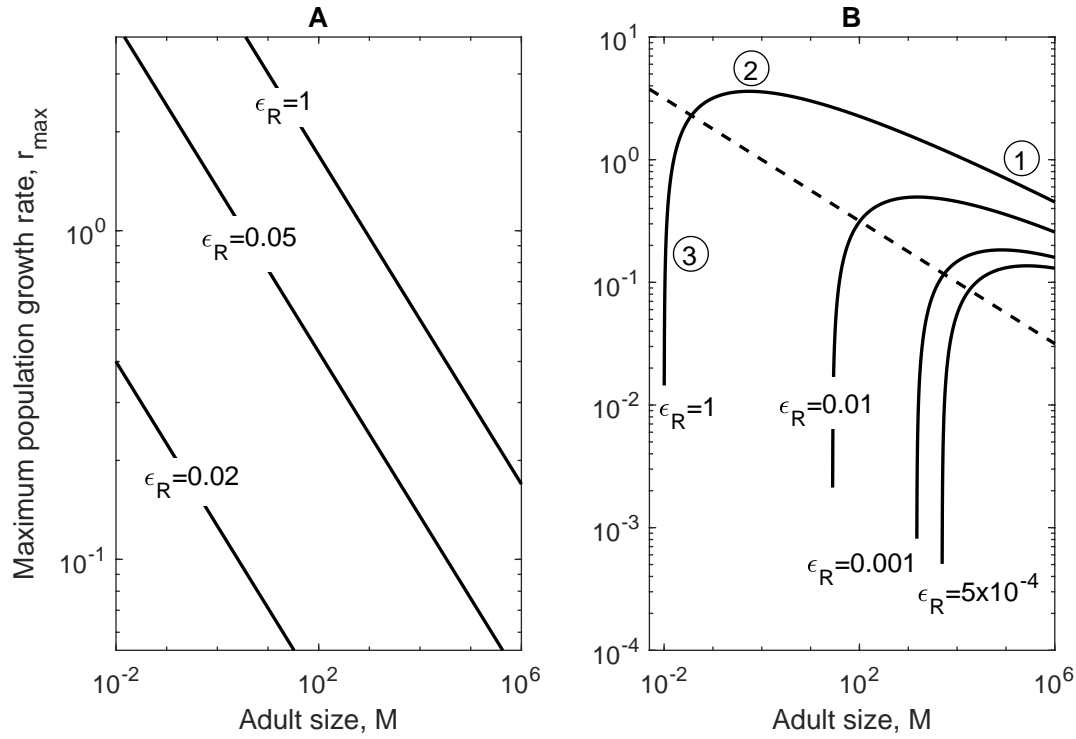


Figure S.B1: Maximum population growth rate r_{\max} as a function of adult size M for two offspring size strategies: Offspring size proportional to adult size M (A) or independent of adult size (B). The recruitment efficiency ϵ_R is varied for both strategies. Individual growth and mortality are constant: $A = 5 \text{ g}^{1-n}/\text{yr}$ and $a = 0.42 \text{ yr}^{-1}$. Adult:offspring size ratio are $M/M_0 = 10^3$ and $M/M_0 = M/0.01$ for the proportional (A) and constant (B) strategy respectively. The black dashed line in panel B represents the $-1/4$ scaling of the proportional strategy. Numbers on panel B represents the three features of r_{\max} .

Supplement C: Length to weight growth model

In our model we use the weight-based Von Bertalanffy growth model that can be linked with physiological models. The link is the relation between K from the length-based growth

$$\frac{dL}{dt} = K(L_{\infty} - l), \quad (\text{S.C1})$$

and A from the weight-based growth

$$\frac{dw}{dt} = Aw^n - k. \quad (\text{S.C2})$$

Here we follow the methods developed by Andersen et al (2019) to find the relation between these two coefficients in the case of $n = 3/4$. Following this work we can transform the length-based to the weight-based form knowing the relation between length l and weight w : $cl^3 = w$. Then we get

$$\frac{dl}{dt} = \frac{dc^{-1/3}w^{1/3}}{dt} = c^{-1/3} \frac{dw^{1/3}}{dw} \frac{dw}{dt} = \frac{1}{3} c^{-1/3} w^{-2/3} \frac{dw}{dt}, \quad (\text{S.C3})$$

where c is the length to weight coefficient. Assuming that juveniles are small enough (i.e. $l \ll L_{\infty}$), their growth from (S.C1) can be approximated as $dl/dt = KL_{\infty}$. With the same logic we have $dw/dt = Aw^n$ from (S.C2). Then (S.C3) can be rewritten

$$A = KL_{\infty} 3c^{1/3} w^{2/3-n}.$$

Von Bertalanffy argued $2/3$ exponent, metabolic theory $3/4$. In the case of a $2/3$ metabolic exponent, n the relation between A and K does not depend on the size (Andersen et al., 2009). In the case of a $3/4$ metabolic exponent A is then scaling with size $w^{1/12}$. Assuming that growth from length and weight model has to be equal at the maturation size (arbitrary argument from Andersen et al. (2008)), and knowing that at the maturation size $w_m = \eta_m w_{\infty} = \eta_m c L_{\infty}^3$, then we get

$$A = 3Kc^{1/4} \eta^{-1/12} L_{\infty}^{3/4}.$$

Supplement D: Physiological model of food consumption

In this appendix we develop our physiological model of food consumption. Through this model we aim to go a step further in our understanding of population dynamics by integrating a resource dependency. This physiological model of food consumption allows to study how food level plays a role in population dynamics and competition.

An individual's consumption is constrained by its ability to encounter a prey. We define an encounter rate of food scaling with size:

$$V(m) = \gamma m^q,$$

with γ the encounter rate coefficient and q the exponent. We assumed that the realised consumption is driven by resource concentration R and encounter rate $V(m)$ through a type II functional response f :

$$f(m, R) = \frac{V(m)R}{V(m)R + C_{\max}}.$$

We assume that resource consumption equals a fraction f of the maximum consumption C_{\max} . The maximum consumption is constrained by the maximum digestive capacity. Such a fractal system should follow metabolic scaling (West et al., 1997), i.e., $C_{\max}(m) = hm^n$, with h a constant varying across taxa. Therefore when the resource is abundant, i.e., $R \gg C_{\max}$, the realised consumption equals the maximum consumption. Conversely, when the resource is rare, i.e., $R \ll C_{\max}$, the consumption equals the amount of food cleared $V(m)R$. This energy from consumption is partly lost due to assimilation efficiency ϵ_a . A fixed amount $C_{\max}f_c$ of energy is used for standard metabolism. Then the available energy of an organism of size m for growth and reproduction is the remaining energy, after assimilation loss and using for standard metabolism:

$$E(m) = \epsilon_a C_{\max}(f(m) - f_c).$$

Inserting $C_{\max}(m) = hm^n$, we get:

$$E(m) = \underbrace{\epsilon_a h(f(m) - f_c)}_A m^n. \quad (\text{S.D1})$$

This new description of the available energy is proportional to individual size m with a 3/4 exponent if the feeding level is constant.

Supplement E: From max. consumption to somatic growth rate A

Individual population growth rate A can be obtained from maximum consumption C_{\max} using our physiological model of food consumption (Appendix C). Using (S.D1) we get the relationship between individual growth and maximum consumption:

$$A = \epsilon_a C_{\max} (f(m) - f_c) m^{-n}. \quad (\text{S.E1})$$

Assuming a feeding level $f(m) = 0.6$ and knowing the body mass associated to the maximum consumption of each individual from Kiørboe and Hirst (2014) we calculated A for Copepods.

Supplement F: Adult size dependency of growth and R^*

We now introduce a possible cross-species scaling of the coefficient A with adult body mass as $A = A_0 M^b$. Note that this does not invalidate the assumption of metabolic scaling of the available energy $E(m)$ at the level of individuals in (S.D1), but it implies different levels of consumption across species with different adult sizes. The available energy is then:

$$E(m) = A_0 M^b m^n. \quad (\text{S.F1})$$

We introduce this scaling because it is observed in some species groups (Fig. 3A). From this cross-species scaling an adult size dependency is introduced in our physiological model of resource consumption by assuming that h scales with adult size M . We assumed that the two forms of available energy described above ((S.F1) and (S.D1)) should be equal for a given level of resource. We assume that both form of available energy are equal for a standard feeding level $f_0 = 0.6$, leading to the equality: $A_0 M^b = \epsilon_a h(f(m) - f_c)$. Solving this equation we can rewrite h as a function of adult size M :

$$h = \frac{A_0}{\epsilon_a(f_0 - f_c)} M^b, \quad (\text{S.F2})$$

where, A_0 and b represent the growth strategy (Fig. 3A and S.A2). Therefor, there is a trade-off between growth and standard metabolism, due to the proportionality of standard metabolism to the maximum consumption rate, i.e., standard metabolism equals $C_{\max} f_c$. Species for which the consumption is higher (h is higher) exhibit higher loss due to standard metabolism.

An estimation of the level of intraspecific competition is given by finding the level of resource R^* for which the population growth rate r_{\max} is null. In other word R^* is the minimum level of resource to maintain the population, that represent the level of intraspecific competition. Finding R_* for which $r_{\max} = 0$ essentially consists in looking where the feeding level equals the critical feeding level $f(M, R_*) = f_c$. We are solving the feeding level for adult size M since the somatic growth rate A in the population growth rate equation refers to adult available energy. The previous equality leads to the solution

$$R_* = \frac{f_c h(M)}{\gamma(1 - f_c)} M^{n-q}, \quad (\text{S.F3})$$

where f_c is the critical feeding level, n the metabolic exponent, γ and q are the parameters for clearance rate.

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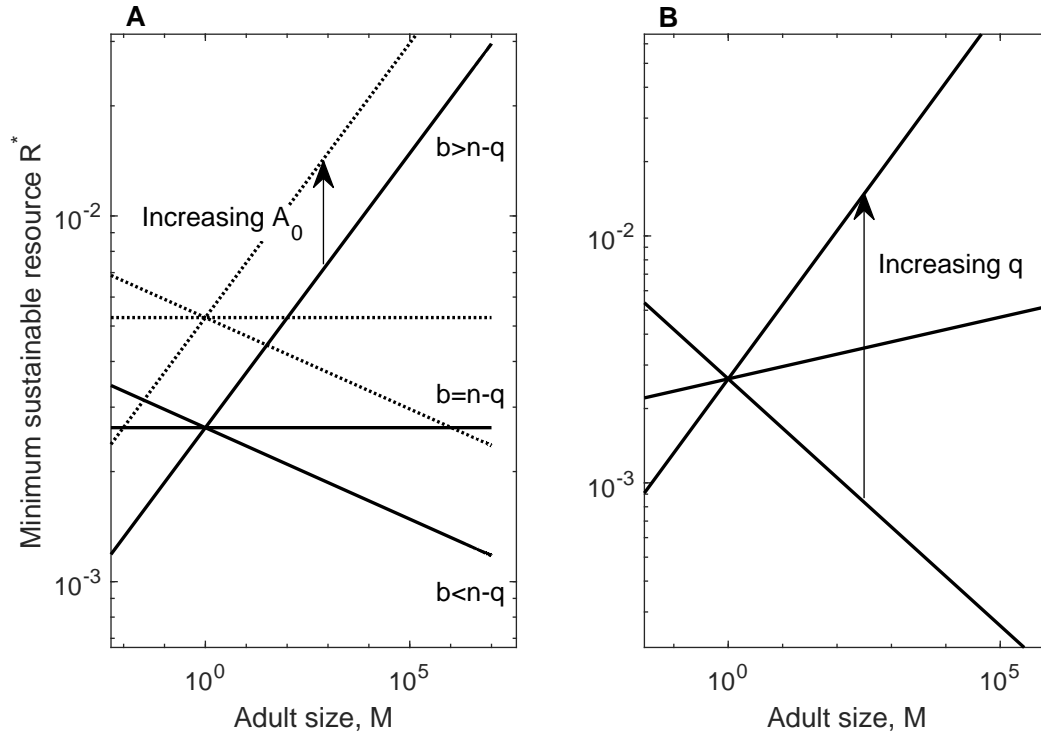


Figure S.F1: Minimum level a resource R_* over adult size M for different growth (A) and encounter exponent q (B). The three growth strategies in (A) are: positive ($b > n - q$), negative ($b < n - q$) or null ($b = n - q$). $n - q$ is fixed when b is varying. We also increased the encounter rate exponent q (B) with A_0 , b and n constant. The minimum resource level does not depend on offspring size strategies, but the growth strategies, i.e., $h(M)$. Form (S.F3) we get that $R_* \propto M^{n-q+b}$, we can then identify three growth strategies b changing the dependency of R_* with adult size M in the case of constant q : 1) $b = n - q$, then the growth does not depend on adult size M . 2) and 3) $b >$ or $< n - q$, therefor the growth increases or decreases respectively with adult size M . Essentially, A_0 determines the overall minimum sustainable resource level (A solid vs dotted lines). We also show that if the growth strategy is constant, changing clearance rate scaling with size (q) produces similar patterns (B).

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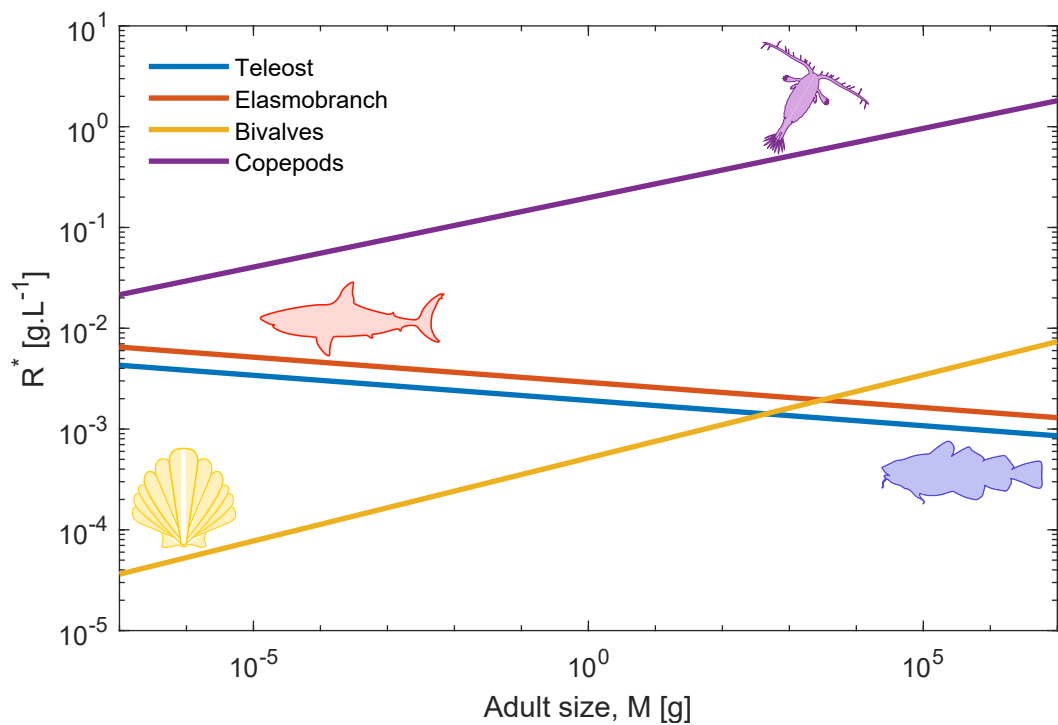


Figure S.F2: Minimum sustainable resource level for telost, elasmobranch, bivalve and copepod.

Supplement G: Relationship between asymptotic and maturation weight.

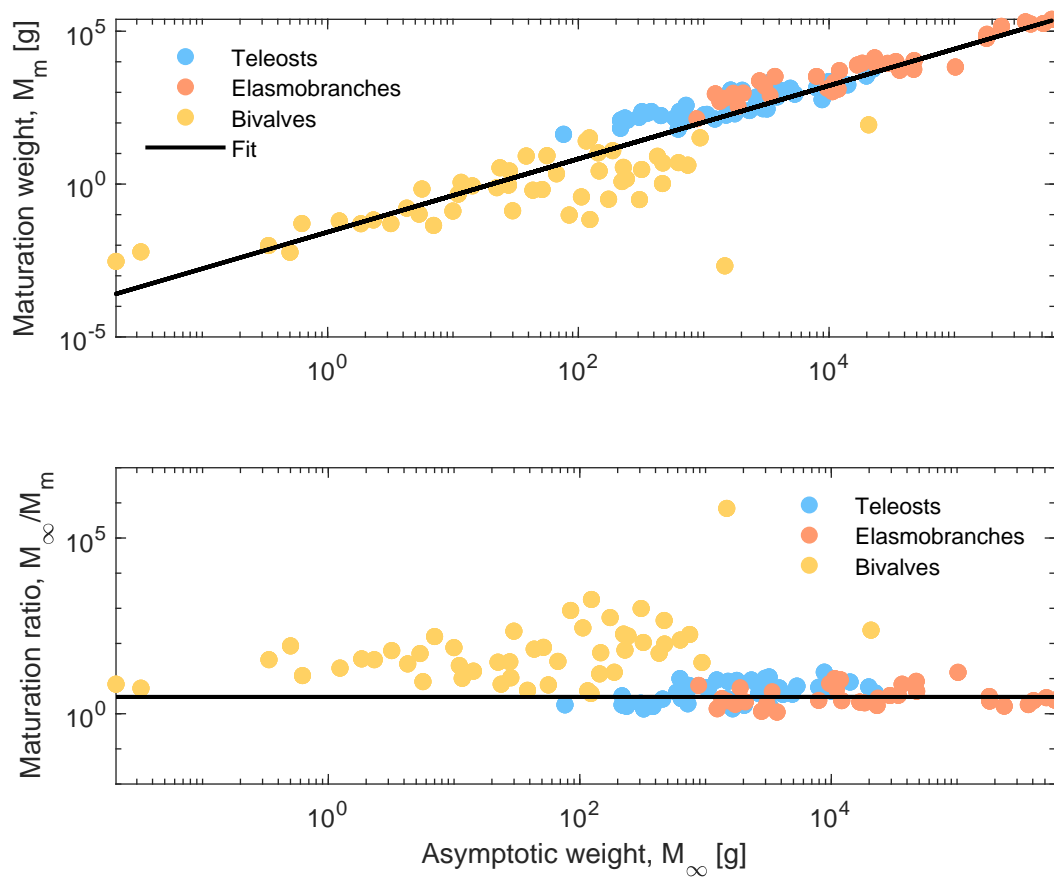


Figure S.G1: Maturation weight is scaling with asymptotic weight with an exponent of 1. The ratio between maturation size and asymptotic size is constant with asymptotic size

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