

Deriving Population Scaling Rules from Individual-Level Metabolism and Life History Traits

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ABSTRACT: Individual metabolism generally scales with body mass with an exponent around $3/4$. From dimensional arguments it follows that maximum population growth rate (r_{\max}) scales with a $-1/4$ exponent. However, the dimensional argument implicitly assumes that offspring size is proportional to adult size. Here, we calculate r_{\max} from metabolic scaling at the level of individuals within size-structured populations while explicitly accounting for offspring size. We identify four general patterns of how r_{\max} scales with adult mass based on four empirical life history patterns employed by groups of species. These life history patterns are determined by how traits of somatic growth rate and/or offspring mass relate to adult mass. One life history pattern—constant adult-to-offspring mass ratio and somatic growth rate independent of adult mass—leads to the classic $-1/4$ scaling of r_{\max} . The other three life history patterns either lead to nonmetabolic population growth scaling with adult mass or do not follow a power-law relationship at all. Using life history data on five marine taxa and terrestrial mammals, we identify species groups that belong to one of each case. We predict that elasmobranchs, copepods, and mammals follow standard $-1/4$ power-law scaling, whereas teleost fish and bivalves do not have a pure power-law scaling. Our work highlights how taxa may deviate from the classic $-1/4$ metabolic scaling pattern of maximum population growth. The approach is generic and can be applied to any taxa.

Keywords: individual mass scaling, metabolic theory of ecology, population growth rate, offspring size, somatic growth rate, marine taxa, life history strategy.

Introduction

Metabolism is a fundamental process of all living organisms. Metabolism describes the energy that an individual processes through organelles and allocates to physiological processes such as standard metabolism, digestion, growth,

and reproduction. Metabolism has been demonstrated to follow a power-law relation with body size of organisms—that is, $Y \propto M^n$, where Y is the metabolism, M the body mass, and n the scaling exponent (Kleiber 1932; Brown et al. 2004). The exact value of the metabolic exponent n has been subject to debate; however, it is generally assumed to be around $3/4$, at least within a given species group, as a result of the fractal organization of systems transporting essential materials, such as vascular or pulmonary systems (Haldane 1928; West et al. 1997).

The relationship between individual metabolism and body size implies that population-level properties, like maximum population growth (r_{\max}), are also influenced by body size. Maximum population growth rate indicates the recovery rate of a population depleted to levels where density dependence does not limit population growth. While that condition is rare in nature, r_{\max} is an important parameter for conservation applications, such as wildlife and fisheries management, and for understanding invasion potential. In this context, general theories, such as the metabolic theory of ecology (MTE), provide guidance. Following the classic MTE framework, maximum population growth rate scales with body mass M with an exponent $-1/4$ —that is, $r_{\max} \propto M^{-1/4}$ (Brown et al. 2004; Savage et al. 2004). This prediction largely rests on a dimensional argument: metabolism is a loss of mass and therefore has dimensions of mass per time. Since population growth has dimensions of per time, r_{\max} must scale with mass with a $3/4 - 1$ exponent. The $-1/4$ prediction has been corroborated by empirical observations over a wide range of sizes and types of organisms: unicellular, heterotherms, and homeotherms (Slobodkin 1962; Fenchel 1974; Blueweiss et al. 1978; Kiørboe and Hirst 2014).

The dimensional argument refers only to body mass and does not represent other life history differences between taxa that may affect the scaling of r_{\max} . Savage et al. (2004) refined the dimensional argument to include

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overlapping generations and life span. This refinement did not change the $-1/4$ scaling of r_{\max} . However, neither the dimensional argument nor any of its modifications have considered the importance of offspring size relative to adult size. Some taxa, such as mammals and elasmobranchs, produce offspring that are a factor 100 smaller in mass than adults, whereas other taxa, such as fish, cephalopods, and plants, can have much larger adult-to-offspring mass ratios (Falster et al. 2008; Neuheimer et al. 2015). As an extreme example, offspring of Atlantic bluefin tuna (*Thunnus thynnus*) grow eight orders of magnitude from an offspring mass of 6×10^{-4} g to a maturation mass around 10 kg. Such differences in adult-to-offspring mass ratio imply that two species with the same adult mass can have very different numbers of offspring and therefore possibly different maximum population growth rates.

Here, we scale from individual metabolic rates to maximum population growth rates while explicitly resolving the population size structure to account for differences in adult-to-offspring size ratios. Our approach is based on metabolism and the scaling of growth and mortality with individual body mass, following classic life history theory (Charnov 1991; Charnov et al. 2013) and recent developments in metabolic life tables (Burger et al. 2019, 2020). To derive the theoretical maximum population growth rate, we use three traits (adult mass, offspring mass, and somatic growth rate) and two parameters (mortality and reproductive efficiency). Through a data analysis of how offspring mass and somatic growth rate covary with adult mass within broad groups of taxa—teleosts, elasmobranchs, bivalves, copepods, and mammals—we identify four general patterns of how maximum population growth rate r_{\max} scales with adult mass. One of the r_{\max} scaling patterns follows the $-1/4$ prediction; the others have a different power-law exponent or do not follow a power-law scaling.

Methods

We first derive the maximum population growth rate from metabolic scaling principles at the level of individuals for a size-structured population. We then collect cross-species data for the main traits that enter into the model: adult mass M , somatic growth rate A , and offspring mass M_0 . The data are collected for five groups of taxa and used to estimate how maximum population growth rate scales with adult mass within each group.

From Individual Scaling Laws to Population Growth

The maximum population growth rate, r_{\max} , refers to the growth rate of a population without density dependence (i.e., classic Malthusian growth). For an unstructured

population, r_{\max} is the difference between the rate of production of surviving offspring b and mortality μ : $r_{\max} = b - \mu$. However, the calculation of r_{\max} becomes more complex when considering a structured population where mortality and fecundity are size dependent.

We consider a semelparous size-structured population where adults die after reproduction, as for annual plants and some marine organisms (e.g., cephalopods or salmon). This assumption implies determinate growth where juveniles use available energy only for growth while adults use this entire energy for reproduction (fig. 1A; for iteroparous reproduction and indeterminate growth, see “Discussion”). Because we assume determinate growth, adult mass M represents the total mass at maturation, including reserves and reproductive tissues. Individuals grow from offspring mass M_0 to the adult mass M (fig. 1B). Following Neuheimer et al. (2015), we define offspring mass as the mass at which individuals are independent of parental care. After reaching adult mass, they convert their mass to offspring with an efficiency ϵ_r .

To estimate r_{\max} for a size-structured population, we use scaling principles, that is, scaling of available energy and mortality with individual mass. We assume metabolic scaling at the individual level—that is, available energy $E(m)$ scales with individual body mass m with an exponent n :

$$E(m) = Am^n, \quad (1)$$

where the coefficient A is termed the somatic growth rate. The available energy $E(m)$ (mass per time) represents the energy that is left after consumed food is assimilated, standard metabolism (maintenance cost) and activities are accounted for (fig. 1A; details in supplement D; supplements A–G are available online). The term $E(m)$ is used for growth or reproduction.

We assume that individual mortality (per time) also follows standard metabolic scaling with exponent $n - 1$ (Andersen 2019, chap. 2):

$$\mu(m) = aAm^{n-1}, \quad (2)$$

where the scaling exponent is $-1/4$ for standard metabolic scaling $n = 3/4$. Equation (2) further assumes that the level of mortality is proportional to the coefficient of available energy A from equation (1). This assumption implies a trade-off between growth and mortality where faster-growing individuals (higher A) also have a higher mortality. This trade-off has been shown in Atlantic silversides (*Menidia menidia*), where subpopulations with faster somatic growth rates experience higher predation (Lankford et al. 2001). Similarly, Riessen (2012) shows that defensive spine production in *Daphnia* leads to a decreasing growth rate. The constant a is a nondimensional number specifying the overall level of mortality relative to growth, also called the physiological rate of mortality (Beyer 1989).

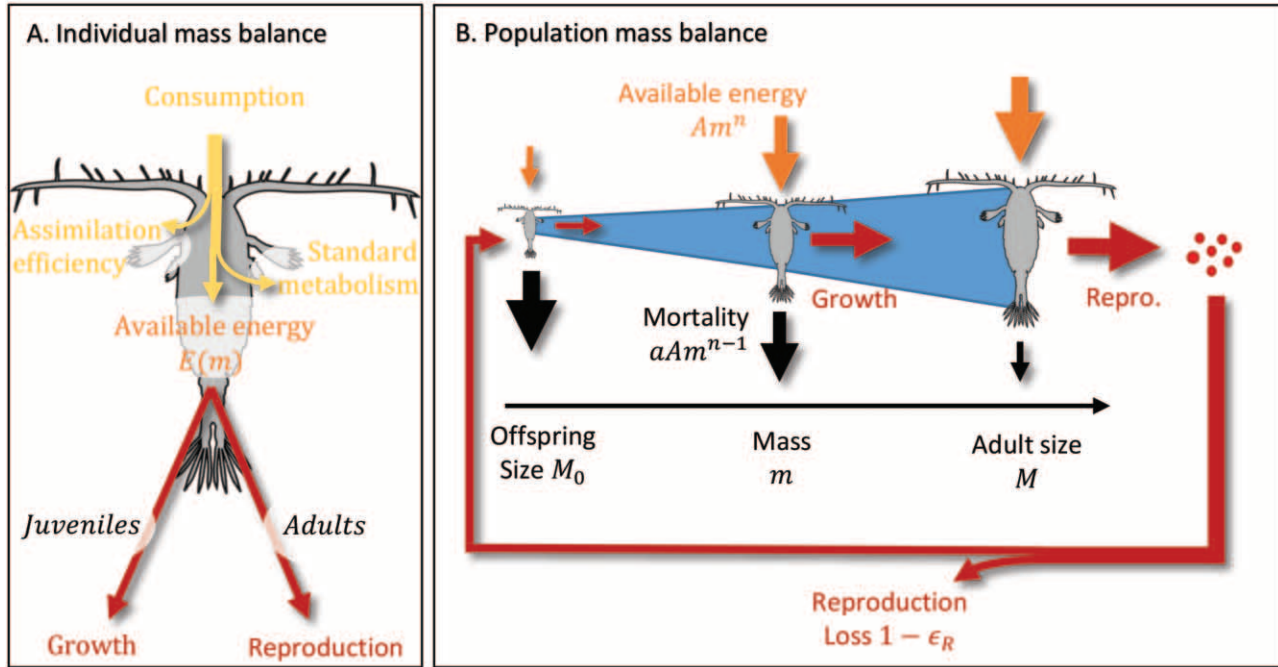


Figure 1: Individual and population mass budgets. The available energy (mass per time) of an individual is used for growth and reproduction and increases with mass as $Am^{3/4}$. Mortality (per time) decreases with mass proportionally to both the mass-specific somatic growth rate A and the physiological mortality constant a . The width of the orange and black arrows indicates how available energy and mortality varies with mass.

The physiological mortality a may be interpreted as a size-based version of the M/K life history ratio (Andersen et al. 2009), where here M refers to mortality and not adult size and K is the von Bertalanffy growth coefficient. The physiological mortality constant may also be derived from size spectrum theory, where it emerges from the balance between the mortality that larger organisms exert on smaller organisms in order to support their metabolism (Andersen and Beyer 2006; Andersen et al. 2009). In this way, the mortality follows directly from assumption (1) and the rule that big organisms eat smaller organisms.

From these three assumptions, we can derive the maximum population growth rate by solving the time-dependent McKendrick–von Foerster equation (McKendrick 1925; von Foerster 1959):

$$\frac{\partial \phi(m, t)}{\partial t} + \frac{\partial E(m) \phi(m, t)}{\partial m} = -\mu(m) \phi(m, t). \quad (3)$$

The McKendrick–von Foerster equation is essentially a classic life table written as a partial differential equation (Andersen 2019, chap. 4). It describes how the juvenile mass distribution $\phi(m, t)$ emerges from the balance between growth $E(m)$ and mortality $\mu(m)$ for all sizes of individuals.

Solving equation (3) requires a boundary condition at the offspring size $m = M_0$ to describe the reproductive

flux of new offspring. Since we assume determinate growth, adults invest all available energy $E(M)$ in reproduction. The reproductive flux in units of numbers per time is then

$$R(t) = \frac{\epsilon_R \phi(M, t) E(M)}{M_0}, \quad (4)$$

where ϵ_R is the reproduction efficiency from available energy $E(m)$ (eq. [1]) to eggs and early-life survival. The reproductive efficiency encapsulates all direct and indirect metabolic costs of reproduction—for example, the building up of reserves, migration and forgone foraging during reproduction, and parental care as well as mortality during the egg stage. We are unable to calculate ϵ_R from scaling principles, as it is determined by reproductive strategies and may therefore vary considerably from population to population. Nonetheless, we expect that there is some regularity within a group of species that share a reproductive strategy (parental care or not, viviparity vs. oviparity, free spawning or not, etc.).

Solving equations (3) and (4) is a matter of standard mathematical analysis, which does not involve further assumptions (supplement B). The solution approximates the maximum population growth rate r_{\max} as

$$r_{\max} \approx A(1 - n)M^{n-1}[(1 - a) \log(M/M_0) + \log(\epsilon_R)], \quad (5)$$

where the approximation is valid for adult size being much larger than offspring size, $M \gg M_0$. The r_{\max} equation combines four important parameters: individual growth A , physiological mortality a , reproductive efficiency ϵ_R , and the adult-to-offspring size ratio M/M_0 .

The r_{\max} (eq. [5]) consists of two terms. The left term, $A(1 - n)M^{n-1}$, scales metabolically with adult size with an exponent $n - 1 = -1/4$. This term is further proportional to the somatic growth rate A , so faster-growing species have a higher population growth rate. Note that species with a faster somatic growth rate also have a higher mortality (eq. [2]), but despite the increased mortality the population growth rate is still proportional to the somatic growth rate. The right term, $[(1 - a) \log(M/M_0) + \log(\epsilon_R)]$, is a correction to the metabolic scaling that depends on the adult-to-offspring mass ratio. If offspring size is proportional to adult size—that is, M/M_0 is constant within a species group—then the right term is also constant within the group and the overall scaling of r_{\max} is $\propto M^{n-1}$. However, if M/M_0 varies within the species group, then the classic metabolic scaling rule no longer applies because the correction in the right term varies with adult size M . Whether r_{\max} follows metabolic scaling therefore depends on the offspring size strategy within a species group.

Data Collection

We collect data on somatic growth rate A and offspring size M_0 for five groups of taxa (bivalves, teleosts, elasmobranchs, copepods, and mammals) to determine how these traits covary with adult size. We further collect estimates of r_{\max} (for details on the data collected, see supplement A, table S.A1; tables S.A1, S.A2 are available online).

Data on somatic growth rate A are for teleosts, elasmobranchs, and bivalves derived via the length-based form of the von Bertalanffy growth equation. The von Bertalanffy growth equation describes individual growth by the coefficient K and asymptotic length L_∞ . We converted K and L_∞ to A (supplement C; Andersen et al. 2009; Charnov 2010). Data on A for copepods were derived from observations of maximum ingestion rate from Kiørboe and Hirst (2014; supplement E). Copepods were split into two groups, active and passive feeders, since these have distinct asymptotic size and somatic growth rate A ranges. No data on A were available for mammals. To examine the relationships between somatic growth rate A and adult mass M for the different groups, we use asymptotic weight as a proxy for adult mass for all of the species. When asymptotic weight was unavailable, we converted it from asymptotic length. The somatic growth rate A data are not temperature corrected (see “Discussion”).

Data on offspring size M_0 are from a previous meta-analysis of offspring size strategies among marine taxa (Neuheimer et al. 2015). In cases with multiple observations of the same species, data on somatic growth rate A and offspring size M_0 are averaged per species. An exception is made for copepod somatic growth rate A data, where all observations are used because we have data only for a few species (only three passive feeder species).

Not much data exist on the physiological mortality a . We assume that it does not vary systematically with adult mass within a group of species. This assumption is supported by observations of M/K being independent of adult size for fish (where the M in M/K refers to mortality and not adult mass), although with some variation between taxonomic groups at a smaller level than the overall group (Beverton 1992; Thorson 2020). We use a value of $a = 0.42 \text{ year}^{-1}$, which is found for teleosts and elasmobranchs (Olsson et al. 2016) and is consistent with theoretical derivations (Andersen 2019, chap. 4.4), noting that a higher value may be relevant for copepods (Serra-Pompei et al. 2020, their app. F).

We treat the reproductive efficiency ϵ_R as a free parameter that adjusts the overall level of the maximum population growth rate (see supplement B; fig. 2). As ϵ_R depends on the reproductive strategy (e.g., free spawning in the

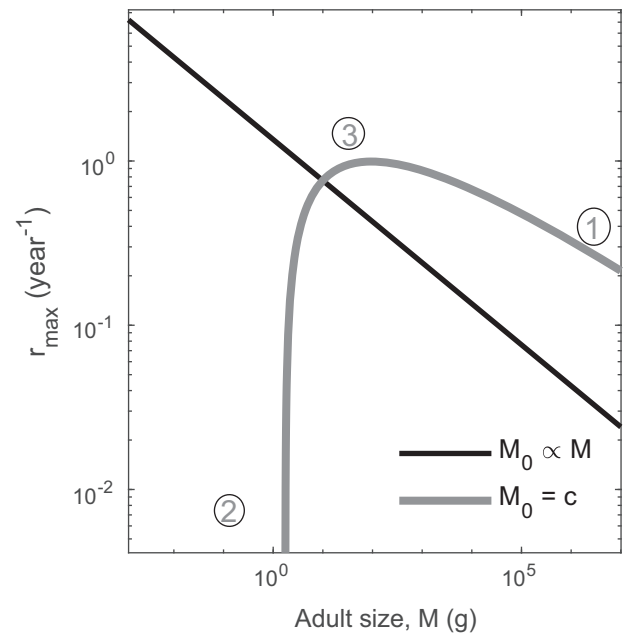


Figure 2: Maximum population growth rate r_{\max} as a function of adult size M for two offspring size strategies: offspring size is proportional to (black line) or independent of (gray line) adult size M . The black dashed line in B represents the $-1/4$ scaling from the metabolic theory of ecology. Numbers represent the three features of r_{\max} for the independent strategy (M_0 is constant).

water column or egg guarding), we assume that ϵ_R is constant within a group (although there are variations within some groups; see “Discussion”). To calibrate ϵ_R , we collect estimates of maximum population growth rates for teleosts, elasmobranchs, and marine mammals (supplement A, table S.A1). It is important to realize that the collected maximum population growth rates are not direct measurements but are model predictions based on data on individual growth, mortality, and reproduction for each population. As such, these estimates come with their own uncertainties and systematic biases. The data are mainly included to calibrate the level of the reproductive efficiency and to compare general trends (i.e., type of scaling of relationships), not for validation of our results. We use an ϵ_R value of 0.03 for teleosts and 0.21 for elasmobranchs to obtain r_{\max} estimates in the same range as the data. For copepods, we use $\epsilon_R = 0.23$, following Serra-Pompei et al. (2020). For bivalves, we use the same value as for teleosts because both groups generally spawn eggs freely in the water column. The parameters used for r_{\max} simulations are provided in table 1. We achieved the simulation using MatLab R2019a. Data and code have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.kkwh70s5v>; Denéchère et al. 2021).

Results

Maximum Population Growth Rate Scaling

The scaling of maximum population growth rate with adult size is determined by the type of offspring size strategy. In the case of proportional offspring size (M/M_0 constant), r_{\max} scales with adult size with an exponent $n - 1$, according to the standard metabolic scaling rule (fig. 2, black line), whereas metabolic scaling no longer applies if offspring size is independent of adult size (M_0 is constant). In the latter case (offspring size independent of

adult size), r_{\max} (eq. [5]) has three features (fig. 2, gray curve). First, if $M \gg M_0$, then $r_{\max} \propto M^{n-1} \log(M)$ (fig. 2, symbol 1). It is therefore no longer a scaling (power-law) relation with adult size but has a logarithmic correction. Second, if M approaches M_0 , then population growth rate decreases to zero. This means that there is a lower limit to the adult size in the group. The lower limit to the adult size is determined by the reproductive efficiency; the smaller ϵ_R , the larger the minimum size (fig. 2, symbol 2). Third, the combination of the features 1 and 2 leads to a maximum r_{\max} at intermediate adult sizes. Therefore, r_{\max} no longer declines monotonically with adult size (fig. 2, symbol 3).

Data Analysis of Somatic Growth Rate and Offspring Size

Within a species group, r_{\max} also depends on how somatic growth rate A varies with adult mass. The results of the data analysis show that for most groups A is roughly constant within the group (copepods, fish, and elasmobranchs), whereas for bivalves A increases systematically with mass (fig. 3A): $A = A_0 M^b$ with exponent $b = 0.21$ (table 1; fig. 3A; table S.A2; $P < 2 \times 10^{-16}$). Somatic growth rate A is also significantly increasing with asymptotic weight for teleosts, but with a much lower exponent of 0.04 ($P = 6.5 \times 10^{-5}$), and in the following we consider A constant for teleosts. Note that A does not correlate with asymptotic weight in elasmobranchs ($P = .70$). For copepods, A does not correlate with asymptotic weight provided that the data are split into two groups of active and passive feeders ($P = .06$ and $.09$ for active and passive feeders, respectively).

Offspring weight of bivalves and teleosts is independent of asymptotic weight (fig. 3B), as the exponents of the relationships are not significantly different from zero ($P = .40$ and $.21$). Conversely, offspring weights of

Table 1: Parameters used for simulation of maximum population growth r_{\max}

Species group	Elasmobranch	Copepod	Teleost	Bivalve	Unknown group
r_{\max} pattern	1	1	2	3	4
A_0 ($\text{g}^{1/4-b} \text{ year}^{-1}$)	5.5	6.36 ^a 2.67 ^b	3.6	.41	.41
b	0	0	0	.22	.22
M/M_0	362.5	176.7	$M/1001 \text{ g}$	$M/(5.3 \times 10^{-7}) \text{ g}$	362.5
ϵ_R	.21	.23	.03	.03	.21
a^c	.42	.42	.42	.42	.42

Note: A_0 and b are the intercept and slope, respectively, of the scaling relationship of growth rate with adult size (i.e., $A = A_0 M^b$). The “Unknown group” column represents an example of strategy 4 with parameter values that are a combination of the bivalve and elasmobranch groups.

^a Active feeders.

^b Passive feeders.

^c Olsson et al. 2016.

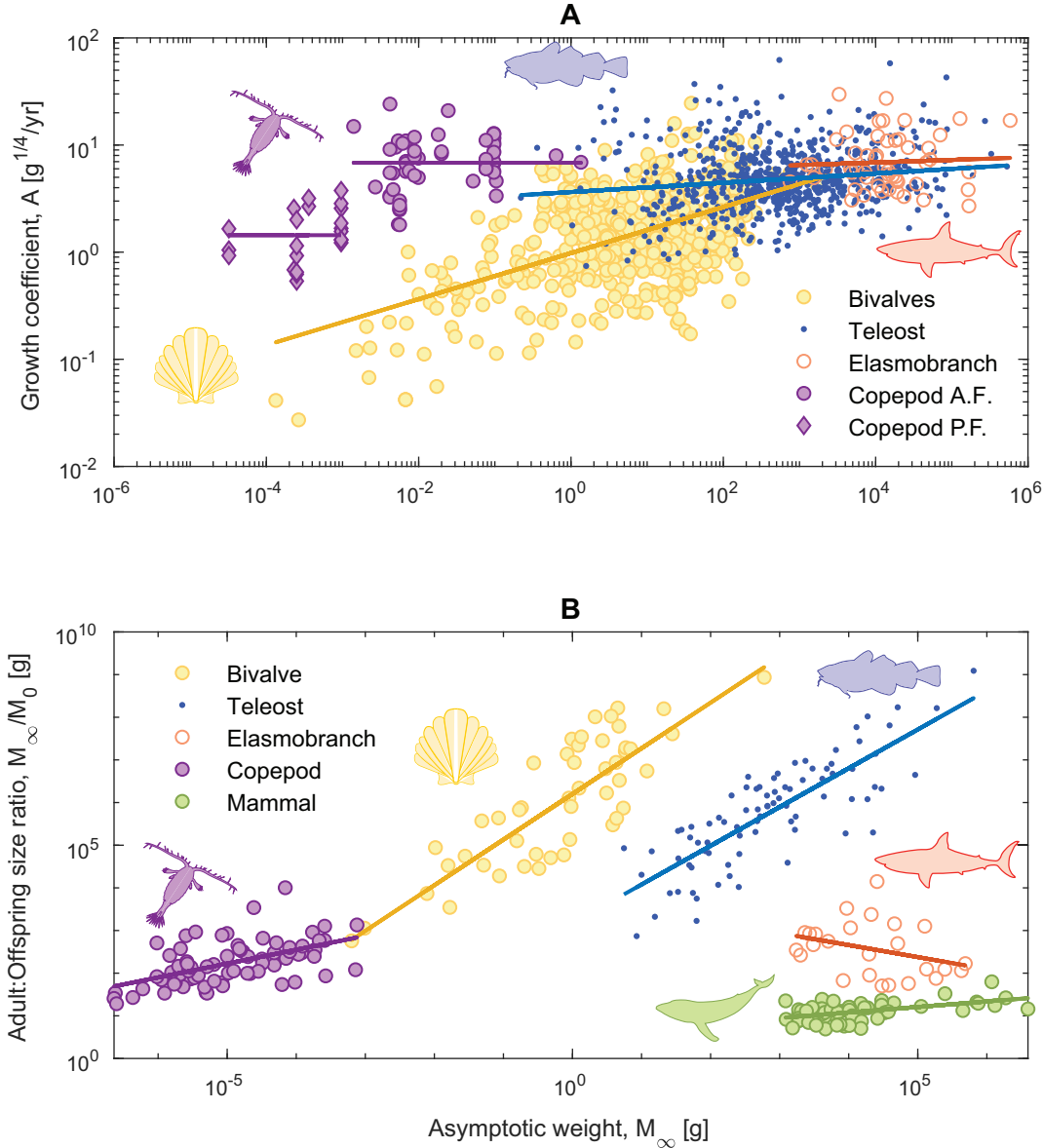


Figure 3: Individual growth (A) and offspring size (B) strategies for five marine groups: bivalves, teleosts, elasmobranchs, copepods, and marine mammals. Statistics of fitted lines are provided in table S.A1. A.F. = active feeders; P.F. = passive feeders.

elasmobranchs, mammals, and copepods increase significantly with asymptotic weight with an exponent varying around 1 (supplement A, table S.A2).

Maximum Population Growth Rate Patterns

In summary, we observe two individual growth strategies A among the marine groups: A either is roughly independent of asymptotic size (teleosts, elasmobranchs, and copepods) or is scaling with asymptotic size (bivalves; fig. 3). Furthermore, we observe two offspring size strate-

gies (Neuheimer et al. 2015): offspring size is either independent of asymptotic size (bivalves and teleosts) or roughly proportional to adult size (elasmobranchs, copepods, and mammals). We refer to these two strategies as the “constant” and “proportional” individual growth/offspring size strategies. By combining these two growth and offspring size strategies, we define four general life history strategies: (1) individual growth is constant and offspring size is proportional to asymptotic weight; (2) both individual growth and offspring size are independent of asymptotic weight; (3) individual growth scales with

asymptotic size and offspring size is independent of asymptotic weight; and (4) both individual growth and offspring size scale with adult weight (proportional strategies). These four life history strategies lead to different patterns of r_{\max} : strategy 1 (proportional egg size and constant growth; fig. 4A, red and purple lines; fig. 4C) is the

only strategy with $-1/4$ metabolic scaling of population growth rate r_{\max} . In contrast, strategies 2–4 differ from the classic metabolic scaling. For strategies 2 and 3, the deviation in r_{\max} scaling is due to a constant offspring size strategy (fig. 4A, yellow and blue lines; fig. 4B). Strategy 4 (proportional egg size and increasing growth) leads to a

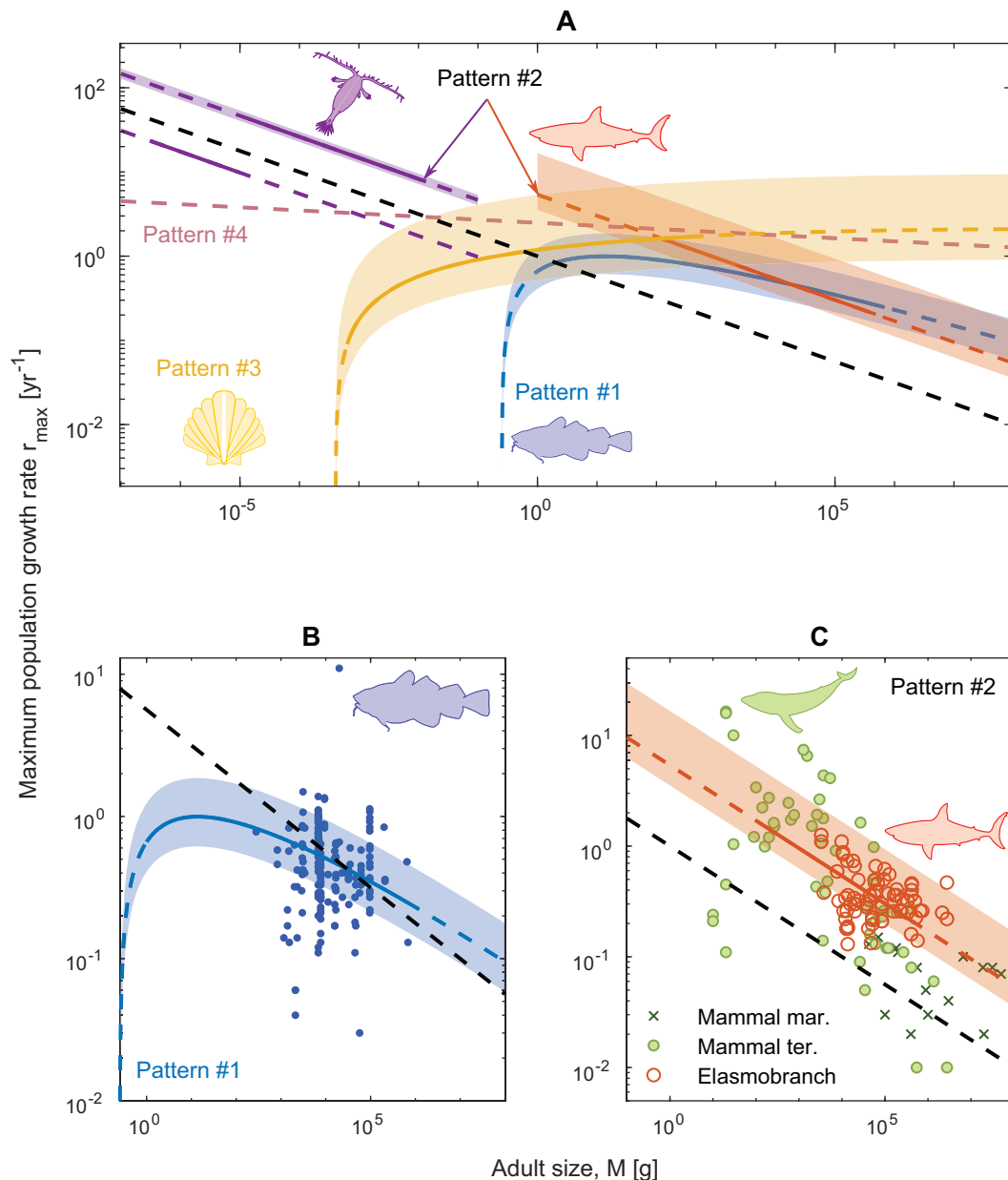


Figure 4: A, Maximum population growth rate as functions of adult mass for the five species groups sorted in the four population growth patterns. B, C, Comparison between prediction and r_{\max} data from Hutchings et al. (2012) for teleosts (B) and for elasmobranchs and mammals (C). Lines are dashed outside the range of observed species in each group. The shaded regions indicate the range of r_{\max} using somatic growth rate A within the confidence interval. The black dashed line represent metabolic scaling, that is, $r_{\max} \propto M^{-1/4}$. Note that the r_{\max} “data” points are not direct measurements but are model predictions from previous studies (see “Methods”), which we used to calibrate the reproductive efficiency parameter in our model.

power law of r_{\max} with a higher exponent than predicted by metabolic theory (i.e., exponent $> -1/4$; fig. 4A, pink line).

Discussion

We have scaled from individual-level metabolism to population-level growth rate r_{\max} . We identified four patterns of how r_{\max} scales with adult mass within a taxonomic group, depending on how offspring mass and somatic growth rate scale with adult mass.

We have estimated the maximum population growth rate under average levels of resources, reproductive efficiency, and mortality and in the absence of density-dependent effects. It is also possible to consider the absolute maximum population growth rate that emerges when resources are available ad lib. and when predation mortality is removed. The absolute maximum population growth rate is found by reestimating somatic growth rate A corresponding to the maximum physiological growth by lowering the physiological mortality a to near zero and by increasing the reproductive efficiency ϵ_R close to 1, to give $\approx AM^{-1/4} \log(M/M_0)/4$. This absolute maximum population growth rate still depends on the ratio between offspring size and adult size and will not qualitatively change the four r_{\max} scaling patterns. The absolute maximum could be relevant for intensively farmed animals or plants or for microbial cultures. The maximum population growth rate that we have estimated throughout the text is relevant for naturally occurring populations, and it is the one we consider in this discussion.

The four scaling patterns show how r_{\max} may vary within broad taxonomic groupings. The r_{\max} of a taxonomic family, genus, or species can deviate from the mean r_{\max} of the group because of taxonomic variation in somatic growth rate (fig. 4, shaded areas), mortality, and reproductive efficiency. For example, *Sebastes* (rockfish) are expected to deviate from the general teleost pattern, as they are slow-growing and late-maturing species with lower than average growth-to-mortality ratios (Thorson et al. 2017). Deviations in r_{\max} may also be population-specific because of environmental conditions that affect growth rate (supplement D), mortality, and/or reproductive efficiency (supplement B). In the following, we concentrate on the general scaling patterns and how they relate to metabolic scaling.

Deviations from Metabolic Scaling

We have shown that species groups follow the metabolic $-1/4$ scaling rule when both the somatic growth rate A and the adult-to-offspring mass ratio are independent of adult mass (strategy 1). We identified three species

groups—elasmobranchs, mammals, and copepods—that follow this prediction. Since a constant adult-to-offspring mass ratio is the most prevalent across marine species groups (Neuheimer et al. 2015) and is found in some terrestrial taxa (e.g., mammals; Falster et al. 2008), we expect that $-1/4$ scaling is common.

Some taxa, such as teleosts and bivalves, may not obey metabolic scaling of maximum population growth rate. This deviation occurs when offspring size is independent of adult size (teleosts, bivalves) and/or when somatic growth rate scales with adult size (strategy 3: bivalves). The deviation from the $-1/4$ r_{\max} scaling emerges because of the explicit accounting of ontogenetic growth and size-dependent mortality. The deviation from metabolic scaling differs from the calculation by Savage et al. (2004), who concluded that maximum population growth rate is approximately scaling with $1/\text{generation time}$ as $M^{-1/4}$, even for overlapping generations. We show that their prediction is correct, but only when offspring size is proportional to adult size.

An additional consequence of the constant adult-to-offspring size ratio (strategies 2 and 3) is the emergence of a minimum body size where a population can have a positive population growth rate. The predicted minimum sizes for teleosts and bivalves are 1 g and 1 mg, respectively. The predicted minimum adult size of 1 mg for bivalves is reasonably close to the smallest bivalve being the *Clinocardium ciliatum* of 0.13 g. Conversely, fish smaller than the predicted 1 g do exist. Many small species—for example, from the families *Gobiidae* (gobies) and *Poeciliidae* (guppies)—employ special reproductive strategies, such as egg guarding or viviparity to a higher degree than larger species (Andersen et al. 2008). Such strategies are designed to increase reproductive efficiency, which is needed for small species to reach a positive r_{\max} (see variation of r_{\max} with ϵ_R in supplement B, fig. S.B1; figs. S.B1, S.F2, S.G1 are available online). Smaller fish species may also achieve a positive r_{\max} by decreasing the physiological mortality a , for example by investing in defense strategies that do not also lower the growth rate substantially.

Another consequence of the constant adult-to-offspring size ratio (in combination with a constant somatic growth rate A with adult size) is the appearance of size where r_{\max} peaks. For teleosts, r_{\max} peaks at an adult size around 100 g. Direct empirical support for this peak is absent. The size does correspond roughly with the peak in maximum demersal fish diversity in the northern Atlantic (around a maximum size of 900 g; Gislason et al. 2020), but it is unclear whether that can be attributed to the peak in r_{\max} .

Evidence for the nonmetabolic scaling of r_{\max} of teleost fish is weak. Independent estimates of maximum population growth rate for teleosts show a constant or weakly

declining relationship for all sizes similar to the metabolic $-1/4$ scaling, although with a large variation (fig. 4A, 4B; Hutchings et al. 2012). Part of this variation is attributed to variation in somatic growth rate, which varies almost a factor 100 from slow-growing rockfish to extremely fast-growing mahi-mahi (dolphinfish; shading in fig. 4). Another independent estimate of r_{\max} over a wider range of fish species (both teleost and elasmobranchs) show an even steeper declining relationship, that is, with an exponent less than $-1/4$ (Thorson 2020). However, that analysis mixes teleosts and elasmobranchs, and since elasmobranchs have low population growth rates and dominate the larger size range, it is unclear whether the finding of a steeper than metabolic scaling relationship holds when these two groups are considered separately. It is worth noting that the maximum population estimates in the above two analyses are not direct observations but are derived from the Euler-Lotka equation using data or estimates of maturity, fecundity, natural mortality, and early-life survival (recruitment at low population sizes). Estimates of mortality and early-life survival are particularly difficult. Mortality is confounded with effects of fishing, which are often substantial for the species that are well studied (and data for mortality were not reported by Hutchings et al. [2012]). Early-life survival is estimated from recruitment at low population density (Myers et al. 1995, p. 327). For large species, recruitment data at small stock sizes are often lacking. This lack of data implies that early-life survival may be underestimated for large species and therefore that their population growth rates could be underestimated. Despite these uncertainties about the estimates of maximum population growth rate, we conclude that there is some empirical support for the predicted minimum size for teleosts and bivalves, but there is disagreement between our general theoretical prediction and independent estimates of maximum population growth rates of larger teleosts.

Bivalves' Individual and Population Growth Increases with Adult Size

Bivalves are the only group where the predicted maximum population growth rates increase with adult size. This prediction raises the question of why bivalves with a small adult size exist in nature. Bivalves are filter feeders, and all sizes compete for the same food in the form of suspended particles. In that case, the species with highest maximum population growth rates will dominate, that is, the largest species. Yet smaller bivalves exist. We hypothesize that smaller species are better competitors for food by being able to survive under conditions of lower food concentrations; they have a smaller R^* sensu Tilman (1980). By extending our model to include resource utili-

zation (supplements D, F), we are able to calculate R^* as the lowest resource concentration where $r_{\max} = 0$ as a function of adult size. We find that smaller bivalve species indeed have smaller minimum resource requirements and will therefore be able to outcompete larger species in a stable environment that is characterized by a low food concentration (supplement F, fig. S.F1).

One can also consider the increasing r_{\max} with adult size of bivalves in the context of the r - K continuum. The distinction between r and K strategies is commonly made with reference to the maximum population growth rate (Pianka 1970). Following that logic, larger bivalves are r strategists, while smaller ones are K strategists. That is uncommon because within a species group, larger species are commonly considered K strategists and smaller ones r strategists (Pianka 1970). However, there are additional considerations to the r - K strategy: for example and as discussed above, larger species have a longer lag to reach maturation, which makes it harder for them to be first colonizers and therefore true r strategists. Nevertheless, it is remarkable that r_{\max} increases with size within a group, and this prediction deserves further attention.

The increasing r_{\max} with adult size is the consequence of another surprising finding of bivalves: their somatic growth rate A increases with adult size (fig. 3). There is yet no understanding of this growth strategy. An increasing growth rate A with adult size implies that at a given individual body size a large species grows faster than a small species, which is not expected from metabolic scaling (see supplement F, eq. [S.F1]). The increase in growth rate A can arise from either increasing consumption with adult size or decreasing costs of other processes, such as defense (shell production). We hypothesize a trade-off between growth and defense that is constrained by growth potential. Within this hypothesis, large bivalve species will tend to prioritize growth to reach large sizes quickly and outgrow a high predation mortality. Conversely, small species, with no potential of becoming large, will invest more in defense (thicker shell) and/or safe feeding behaviors. However, there is no support for this hypothesis across differently sized species. Studies have found that individual bivalves can change their behavior to avoid predation by reducing feeding activities (Griffiths and Richardson 2006) and/or increasing burrowing (de Goeij 2001; Van Gils et al. 2009; Nuñez et al. 2014).

Limitations and Caveats

Our theoretical model is based on simplifications. We assume a semelparous population, that is, a population in which individuals die after the first reproduction. This assumption implies two hidden assumptions about the ratio between asymptotic size and maturation: it is independent

of adult size and equal to 1 ($M_{\infty}/M_{\text{mat}} = 1$). We show that $M_{\infty}/M_{\text{mat}}$ is indeed constant in supplement G, fig. S.G1. However, iteroparous strategies are abundant (all mammals, birds, some fish). Some further employ an indeterminate growth strategy and continue growing after maturation (like fish and most plants). It is mathematically possible to account for iteroparous and/or determinate growth; however, the mathematical solution is fairly complex (Andersen 2019, chap. 7, fig. 7.1). The solution involves a correction that is a function of the constant ratio of asymptotic and maturation size. Yet the correction does not depend on body size and will hence not affect the general shape of our solution.

We based our calculations on metabolic scaling and used the canonical exponent $n = 3/4$. However, there may be deviations from the classic 3/4 exponent within taxonomic groups. For example, growth of fish is often described with $n = 2/3$. Using a 2/3 exponent (von Bertalanffy 1957) would lead to a correction in the scaling of r_{max} (i.e., $r_{\text{max}} \propto M^{-1/3}$); however, it would not qualitatively change the large difference in r_{max} scaling between groups with offspring size proportional to or independent of adult size. Furthermore, the observed increase in A for bivalves (0.22) is significantly larger than the difference between an exponent of 3/4 and 2/3 (0.09). The scaling of A with adult size would therefore remain positive.

An underlying assumption of the scaling exponent n of available energy $E(m)$ is that activity and standard metabolic costs scale with the same exponent as standard metabolism (supplement D, eq. [S.D1]). If activity scales with a higher exponent than n , an upper size limit can be derived where r_{max} goes to zero (Andersen et al. 2008), similar to the lower limit for species with constant offspring size. This upper limit occurs at the adult size where available energy $E(m)$ and activity metabolism are equal.

For the data analysis, we have not temperature corrected our estimates of somatic growth rate A . If the adult size was systematically biased with temperature, the relationship between individual growth A and adult size M —constant or scaling—could be affected. In other words, if the large species in our data analysis are living at relatively low latitudes and small species at high latitude. Reanalyzing available growth-temperature (or latitude) data for bivalves, teleosts, and elasmobranchs (Moss et al. 2016; van Denderen et al. 2020) shows no support for a systematic bias of growth rate with temperature in teleosts and elasmobranchs. Therefore, we do not expect that variation in teleost and elasmobranch growth as a result of temperature would affect the A - M relationship. For bivalves, previous work with the same bivalve data set has found a weak effect of temperature on the product of L_{∞} and K that approximates A (Saulsbury et al. 2019; Reed et al. 2020).

Conclusion

We have developed a general derivation of population growth rate of any population from three traits: adult mass, offspring mass, and somatic growth rate. Our work extends classic predictions from MTE by accounting for ontogeny and variation in life history patterns. We identified key strategies that allow determining whether taxa are likely to follow the classic $-1/4$ metabolic prediction of maximum population growth or deviate from it. Our approach is general and can be applied to all living organisms.

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Statement of Authorship

All authors designed the model methodology. R.D. performed the research (data collection, data analysis, and coding simulation). All authors contributed to writing. Supervision was performed by K.H.A. and P.D.v.D.

Data and Code Availability

Data and code are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.kkwh70s5v>; Denéchére et al. 2021).

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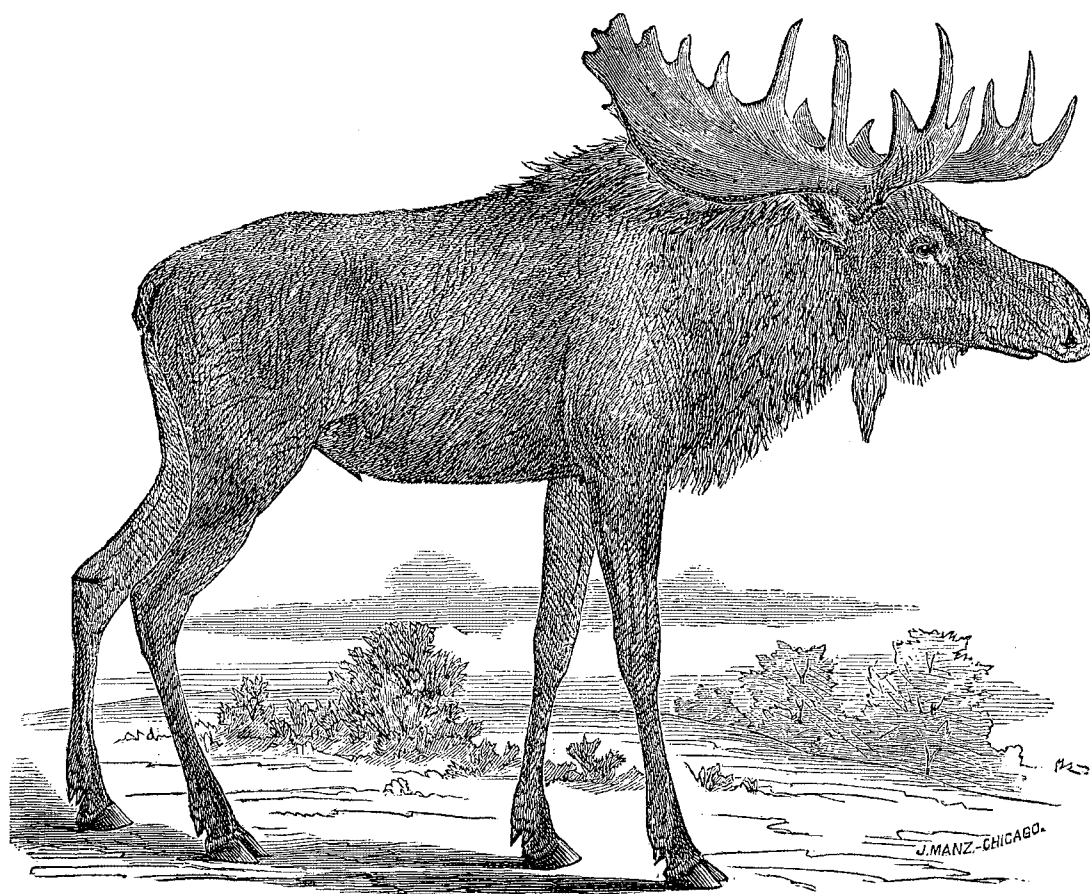
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“The author is well known to have devoted much time and care to the study of the *Cervidae*, and has already published many articles on the subject which have shown him to be a close and accurate observer, and have made him the highest authority in this country respecting all that relates to the natural history proper of these valuable and interesting quadrupeds.” Figured: “Male Moose.” From E. Coues’s review of Caton’s *Deer of America* (*The American Naturalist*, 1877, 11:354–358).