Trends in Ecology & Evolution

Opinion

Have We Outgrown the Existing Models of Growth?

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Theories of growth have a long history in biology. Two major branches of theory (mechanistic and phenomenological) describe the dynamics of growth and explain variation in the size of organisms. Both theory branches usually assume that reproductive output scales proportionately with body size, in other words that reproductive output is isometric. A meta-analysis of hundreds of marine fishes contradicts this assumption, larger mothers reproduce disproportionately more in 95% of species studied, and patterns in other taxa suggest that reproductive hyperallometry is widespread. We argue here that reproductive hyperallometry represents a profound challenge to mechanistic theories of growth in particular, and that they should be revised accordingly. We suspect that hyperallometric reproduction drives growth trajectories in ways that are largely unanticipated by current theories.

Do We Understand Body Size As Well As We Think?

Body mass is a universal feature of all organisms, varies across 21 orders of magnitude, and has fascinated biologists for centuries [1]. Body mass covaries with most of the key physiological, ecological, and evolutionary parameters. For example, larger organisms have lower mass-specific metabolic rates and tend to live for longer than smaller organisms [1]. Larger organisms have lower intrinsic rates of increase and population sizes, smaller effective population sizes, and lower rates of evolution than tiny organisms [1]. Body mass shows conspicuous macro-ecological patterns, covarying with latitude, temperature, and mode of life [1]. Despite its importance and its commonality to all animals, we argue that we still have a remarkably poor understanding of the drivers of body size. In this opinion article, we briefly describe the two major branches of theory concerning growth, their similarities and differences, and discuss how a recent empirical discovery challenges the core assumptions of both.

Understanding Growth and Reproduction

Bottom-Up (Mechanistic) Approaches

Theoretical attempts to understand ontogenetic changes in body size (growth) have a long history [2–14], and debate continues to rage about the mechanistic validity and utility of theories of metazoan growth [15–22]. The most venerable of these theories was proposed by Püttér [2], but is now most commonly associated with von Bertalanffy [3,4,23,24]. The von Bertalanffy growth function (VBGF, see Glossary) estimates the rate of increase in mass (growth) as the difference between rates of ‘anabolism’ and ‘catabolism’, where the rate of catabolism is proportional to mass m, and the rate of anabolism is proportional to \( m^\beta \), where \( \beta \) is positive and less than 1. Although von Bertalanffy considered a range of potential values for \( \beta \) [4], a value of 2/3 is the most common based on the assumption that synthesis is proportional to the uptake of resources over a resorbing surface [3]. The mechanistic interpretation of the VBGF has shifted through time, and it has since been variously restated as representing the difference

Highlights

Most models of growth assume that reproductive output scales proportionately with body size. However, a recent meta-analysis of fish contradicts this assumption, and shows that reproduction scales hyperallometrically across a wide variety of taxa.

Hyperallometric reproduction represents a profound challenge to most mechanistic theories of growth.

We argue that growth slows not because of mechanistic constraint but because of increasing allocation to reproduction, and that many models of growth have been seeking to understand the wrong phenomenon.

Resolving these issues has major implications for how we manage and harvest species, and predict the impacts of global change on the productivity of biological systems.
between rates of energy assimilation and expenditure (e.g., [25,26]), or the difference between the rates of energy use for metabolism (including growth) and maintenance (e.g., [27]). These considerations generate the impression of a sound theoretical foundation for the VBGF. Oddly, however, the VBGF does not consider reproduction at all. The exclusion or minimisation of the role of reproduction in mechanistic models of growth continued well beyond von Bertalanffy and into extant models today.

The mechanistic framework used in VBGF to understand the slowing of growth to a final or asymptotic size started a school of thought that focused on ‘bottom-up’ drivers of growth and body size. Under this framework, body size is the product of proximal, mechanistic constraints on resource supply and demand. Variations of this approach have proliferated ever since, and include well-known frameworks such as dynamic energy budget (DEB) theory [6], the ontogenetic growth model (OGM) [7,9,12], and Pauly’s limiting gill surface model (LGSM) [11]. Although each has different foci and emphases, each of these models essentially assumes that the size-dependence of resource (energy or oxygen) acquisition is shallower than the size-dependence of resource use, such that these two relationships eventually converge and growth ceases (Box 1). In other words, growth slows or ceases at some asymptotic size because the organism is no longer able to acquire [3,4,6,11,23], distribute [7,9,12], or use [3,23] resources faster than it expends on self-maintenance. VBGF, DEB, OGM, LGSM and other mechanistic models often do an excellent job of describing the slowing of growth of most organisms as they approach a final or asymptotic size (Box 1).

As was pointed out over 20 years ago [28], despite their fit to the data, the mechanistic inferences derived from bottom-up models are problematic because such models fail to adequately consider reproduction. Reproduction is costly, both in terms of mortality risk and energy — reproductive tissues can represent up to 75% of body mass in highly fecund invertebrates [29]. The onset of reproduction therefore involves very different mechanistic dynamics than the preceding juvenile phase as resources are shunted from growth to reproduction [28]. Most mechanistic models make a simple but absolutely crucial assumption: that reproduction is proportionate to body size — in other words, reproduction energy output scales isometrically with size. These models assume that allocation to reproduction occurs from birth and remains a constant fraction of total body size throughout ontogeny (Table S1 in the Glossary).

### Dynamic energy budget (DEB) theory

A mechanistic model of growth to quantitatively describe mass and energy budgets at the level of organisms. It has numerous assumptions about energy uptake, storage, and utilisation. Similarly to VBGF, growth slows down in this framework because of energy dynamics rather than because of increasing allocation to reproduction.

### Hyperallometric reproductive scaling

An empirical relationship between reproductive energy output and body size (mass) for mature individuals that has a scaling exponent greater than 1.0. If reproduction is hyperallometric, then larger individuals reproduce disproportionately more than smaller individuals.

### Integral projection models

A class of demographic population models that allow for continuous stage structure and heterogeneity among individuals. Life-history variables are linked to vital rate functions to produce demographic parameters for populations or individual phenotypes.

### Isometric reproductive scaling

An empirical relationship between reproductive energy output and body size (mass) for mature individuals that has a scaling exponent that is 1.0. If reproduction is isometric, then larger individuals have the same relative reproductive energy output to smaller individuals. Note that models assuming isometric allocation to reproduction generally apply across the entire life history, and not only post-maturity.

### Mechanistic models of growth

There is no absolute definition of what constitutes a mechanistic versus phenomenological model of growth. For our purposes, we define mechanistic models of growth as those that parameterise models based on explicit physiological mechanisms and focus on state variables that alter physiology (e.g., temperature) rather than affecting selection (e.g., mortality risk) on body size.

### Ontogenetic growth model (OGM)

A mechanistic model of growth based on assumptions about the drivers of metabolic scaling and constraints on resource distribution. The model assumes that allocation...
to reproduction is a constant proportion of size, begins at birth, and remains unchanged by ontogeny.

**Pauly’s limiting gill surface model (LGSM):** a mechanistic model of growth for aquatic organisms, particularly fish, in which the acquisition of oxygen is limited by gill surfaces. The model assumes that, because the ability to acquire oxygen by gills scales with size less steeply than oxygen demands scale with size, growth slows as larger individuals approach their physiological limits. Reproduction plays no role in the slowing of growth.

**Phenomenological models of growth:** it is impossible to definitively argue that one model is mechanistic and another is phenomenological. We define phenomenological models as those that focus on how external state variables alter selection on life histories, and how life histories are optimised given assumed constraints and trade-offs.

**Reproductive energy output:** the total reproductive output (number × size × energy content of offspring) by individual per unit time.

**von Bertalanffy growth function (VBGF):** a model that describes the growth of an organism with the underlying mechanistic assumption that growth slows down because the rate at which resources are acquired cannot keep pace with the rate at which resources are required. Reproduction is assumed to play no role in growth dynamics.

supplemental information online) that is unchanged before and after reproductive maturity. As we shall show later, such assumptions are unrealistic and contradicted by data. Note that we have not included a discussion of information-based models of growth, but these models also tend to disregard the costs of reproduction.
Top-Down (Phenomenological) Approaches

Life-history theory assumes that organisms evolve to maximise their reproductive output, and that life-history strategies are the product of optimising various trade-offs among many competing traits for the allocation of key limiting resources [28,30]. In contrast to mechanistic approaches, life-history theory tends to make simplifying assumptions about how the limiting resources are acquired or can be deployed. For example, such theories might assume that the production of new tissue must scale with body mass [28,31], or that resource acquisition scales with body size in particular ways [32], while remaining agnostic as to why such scaling occurs. Phenomenological, life-history models assume that the external context of the organism drives the optimisation of growth and reproduction (and hence size) within the constraints of assumed trade-offs [33]. Thus, size at maturity is predicted to be inversely related to mortality rate under a simple life-history model [30]. From this perspective, life-history models are ‘top-down’ – they are driven by selection on body size, and the underlying physiology evolves in response to these selection pressures. Such phenomenological models of growth are good at predicting changes in size, based on variation in external context across populations or between closely related species (e.g., [34,35]).

Phenomenological and mechanistic models are the two major branches of theory that consider growth and body size, but there have been several attempts to combine them. One group, broadly classed as biphasic models (reviewed in [36]), considers the mechanistic drivers of growth before and after maturity separately. Similarly, links between DEB theory and integral projection models consider the demographic consequences of different physiologies [37]. These hybrid approaches seek to maximise their relevance and explanatory potential by drawing the different strengths of both the mechanistic and phenomenological schools of thought about how and why organisms grow. Thus, models of growth occur along a continuum, from exclusively mechanistic to exclusively phenomenological, but most tend to make assumptions about the costliness of reproduction.

Most Mechanistic and Life-History Models of Growth Assume Reproductive Isometry

As the above makes clear, there is tremendous diversity in the theories we use to understand body size. Despite this diversity, most models assume that reproductive output scales directly and proportionally to size (Table S1).

Of the major branches of theory, the mechanistic models in particular tend to have a core assumption that the fraction of energy allocated to reproduction remains unchanged from birth to death. Under these models, growth slows because resources become more limited, not because more resources are directed to reproduction. Were these models to have increasing allocation to reproduction, net resource flux would become negative and the organism should shrink. Phenomenological and biphasic models tend to have different dynamics for growth before and after maturity. Before maturity, growth in these models is unaffected by reproduction because it is either excluded or the costs are insignificant. After maturity, increasing allocation to reproduction reduces growth (Table S1). Phenomenological models typically allow reproductive scaling to emerge from the model rather than assuming its form a priori and a wide array of reproductive scaling exponents have been predicted – spanning hypoallometry, isometry, and hyperallometry. Two questions therefore seem to be worth asking. (i) How reasonable is an assumption of isometric reproductive output (isometric reproductive scaling)? (ii) If reproduction is not isometric, how does this alter our understanding of growth?
Reproductive Hyperallometry Is Probably Common

We define reproductive hyperallometry as the intraspecific relationship between **reproductive energy output** per unit time and body size for mature individuals experiencing the same conditions. Such a definition best matches theories of growth. A recent study showed that, for 342 species of fish across 15 orders, fecundity scales hyperallometrically for most [38]. For 95% of fish species in the study, larger mothers have disproportionately higher reproductive output via fecundity effects, offspring size effects, or both. For marine fish it therefore seems that hyperallometric reproduction is the rule, but does it occur more generally?

Initial indications are that hyperallometric reproduction is not restricted to marine fishes (Figure 1). A compilation of weight–fecundity relationships for 23 species of freshwater fish found a mean exponent of 1.08 [39]. Mass–fecundity scaling exponents are often greater than 1.0 for invertebrates from a range of phyla (mean ± S.E. for mussels, $\beta = 1.42 \pm 0.17$; sea urchin, $1.224 \pm 0.048$ [40]). For 20 species of crab, a range of scaling exponents have been reported, ranging from $\sim 1.0$ to 1.4, with most sitting above 1.0 [41]. Some taxa show relatively extreme hyperallometry; for example, four species of congeneric bugs show scaling exponents of mass and fecundity between 5.1 and 7.8 [42]. Importantly, the studies described here, other than Barneche et al. [38], only examine the scaling of fecundity. The true costs of reproduction are the number and the energy content of offspring, and estimates of reproductive scaling should ideally include both. Estimates of offspring energy content within species are rare, but, for marine fish at least, both fecundity and per offspring energy content scale hyperallometrically with body size [38]. We are not aware of any other compilations of how offspring energy content scales with body size within species, but Lim et al. [43] show that larger mothers tend to produce larger offspring (with presumably more energy) across a wide variety of taxa. It seems likely therefore that estimates of fecundity should estimate the lower bound of reproductive scaling.

We suspect that reproductive hyperallometry is the rule for most taxa, but it has simply been overlooked. Extensive and formal meta-analyses will be necessary to confirm or contradict this suspicion. We anticipate that there will some species with isometric or even hypoallometric reproduction, and determining patterns and drivers of deviations from hyperallometry will be an interesting challenge. At this point it seems reasonable to suggest that hyperallometric reproduction is the rule in a major taxonomic group (marine fish) and, at the very least, also occurs in a wide range of other taxa. Based on these patterns of reproduction, we would argue that theories of growth should be modified.

What Does Reproductive Hyperallometry Mean for Theory?

Mechanistic models of growth are particularly vulnerable to the violation of the assumption of reproductive isometry. As Roff [44] shows, deviations from isometric reproduction profoundly alter the predictions of growth models: increasing allocation to reproduction slows growth more rapidly than many models predict, leading to negative growth or shrinkage (sensu [44]). The first version of the OGM [7] explicitly assumes that reproductive allocation is isometric and that the energy density of eggs stays constant across ontogeny (an additional assumption contradicted by [38]). Under these assumptions, OGM predicts that reproduction should not qualitatively affect the trajectory of growth, instead it should simply lower asymptotic size. Incorporating both an increasing allocation of body mass to reproduction and changes in energy density of eggs means that such equations (equation 5 in their paper) no longer apply. Instead, growth would be predicted to be negative at larger body sizes. Subsequent updates to the OGM model [9] make no mention of reproduction, and we therefore cannot assess the impacts of incorporating reproductive hyperallometry into these. Charnov et al. [45] retain the assumptions of the...
Figure 1. Relationship between Body Mass (Relative to Largest Individual Measured for That Population) and Relative Batch Fecundity (Relative to the Most Fecund Individual for That Population). (A) For three marine invertebrates (Mytilus edulis shown in green and Strongylocentrotus droebachiensis in light blue, both from [40], and Pocillopora damicornis in dark blue, from [57]). (B) For three terrestrial animals (Gopherus agassizi in yellow, from [58], Rana temporaria in purple, from [59], and Nephotettix virescens in orange, from [42]). In all cases, solid lines depict hyperallometric fit based on data; dotted lines show the often-assumed isometric relationship.

The original OGM with regards to isometric reproduction and, again, the conclusions of this model must change when reproductive hyperallometry is included. DEB models allow for reproductive hyperallometry, and some explicitly predict it [46], but it has been argued strongly that a fixed allocation to reproduction (reproductive isometry) is the best assumption [47].
It seems that many of the influential ‘bottom-up’ models of growth need revising in light of the finding that reproduction is often hyperallometric. These models had a decreasing relative resource supply function ‘hardwired’ into them such that reproduction costs must stay constant or organisms would shrink once they start to reproduce. We would argue that these models are trying to explain dynamics that are driven by increasing allocation to reproduction (Box 1), but they do not allow for it. Whether these models can incorporate reproductive hyperallometry while maintaining other realistic assumptions is unclear.

Some life-history models are more amenable to reproductive hyperallometry, indeed some even require or assume hyperallometry (Table S1). For example, Mangel assumes hyperallometry, and ‘reverse engineers’ a prediction of natural mortality in the field, providing new insights on what has long been thought of as a black box of aquatic ecology (Table S1). Other models predict reproductive hyperallometry. For example, a model by Audzijonyte and Richards predicts that reproductive hyperallometry emerges from reproduction becoming relatively less costly at larger sizes (Table S1). Models by Kozlowski and coworkers, some biphasic models, and the pioneering work of Gadgil and Bossert (who presciently predicted from their model that reproduction should be hyperallometric in fish specifically) all have some parameter space in which hyperallometric reproductive scaling should be favoured (Table S1). We believe that the models of Kozlowski in particular have not received the recognition they deserve – these models anticipated both hyperallometric reproduction and the evolutionary impacts of intense harvesting in fish [35].

Even life-history models often assume that relative scope for reproduction decreases with larger body sizes. The hyperallometry predicted by these models emerges from increased allocation of an ever-decreasing amount (relative to size) of resource to reproduction. More generally, the assumption that relative scope for production decreases with size is perhaps the one assumption common to both life-history and mechanistic models of growth (Table S1). Eighteen years ago, Kozlowski [48] and other since [49] have noted the importance of this assumption for driving the outcomes of a range of models of growth. Given how crucial and ubiquitous this assumption is, it is remarkable how little empirical scrutiny it has received.

The Scaling of Resource Acquisition – An Underexplored Parameter

Relatively few studies estimate the scaling of resource acquisition with body size. Peters [1], in his excellent book, concluded that energy acquisition scales at the roughly same exponent as metabolic rate based on among-species comparisons. If the exponents for acquisition and expenditure are the same, the net scope for production should increase with mass in an absolute sense (contradicting most mechanistic theories of growth) but decrease with mass in a relative sense (if both energy acquisition and expenditure use scale at 0.75, then net scope for production also scales with an exponent of 0.75). Thus, Kozlowski and colleagues [31,50] reasonably followed the conclusion of Peters in assuming scope for production scales hyperallometrically. Interestingly however, Peters’ actual data show that energy acquisition scales slightly higher than energy use (exponents of 0.82 and 0.76, respectively) such that the net scope for production should actually increase in both an absolute and a relative sense (net scope for production should scale as $M^{0.16}$). However using interspecific scaling exponents to infer intraspecific scaling exponents is problematic, and intraspecific comparisons are more informative and direct.

Unfortunately, studies of the intraspecific scaling of ingestion with size remain surprisingly rare. Reiss [51] reports scaling exponents of energy ingestion of between 0.63 and 0.89 for 10 ectotherms, and for some of these species the exponent for ingestion exceeds the exponent for
energy use. Based on this albeit limited number of studies, we would argue that the long-held and highly influential assumptions that available resource flux decreases either absolutely (in mechanistic models) or relatively (in life-history models) with body size require formal re-examination. Such empirical studies exist (e.g., [52,53]) but are rare. Estimating this parameter may also help to resolve unrelated controversies among theoreticians regarding the scaling of ingestion more generally [54,55]. In the meantime, it seems more reasonable to assume that resource intake has a scaling exponent that is at least as high as the metabolic scaling exponent.

Making the simple assumption that both resource acquisition and use have the same exponent, and combining these parameters with hyperallometric scaling of reproductive output, it is remarkable how well growth trajectories can be predicted. Box 1 shows that combining these parameters fits the data for cod Gadus morhua at least as well as the VBGF [3,4,23,24] and OGM [7,9,12]. Table S1 shows that the same is true for an additional 12 species of fish, employing metabolic rate and reproductive scaling exponents taken from published compilations [38,56]. It seems, to us at least, that the growth dynamics that biologists have long sought to understand emerge simply from hyperallometric reproductive scaling.

Concluding Remarks: Where to from Here?
Three important issues for further exploration emerge from this discussion. First, the ubiquity of hyperallometric fecundity scaling should be explored for a broader range of taxa (as well as the scaling of other components of reproductive energy output; Box 2). Second, models across the mechanistic and phenomenological spectrum should be revised to better accommodate hyperallometric reproductive scaling. Third, estimates of the size scaling of energy acquisition and energy use for the same individuals under the same conditions will be necessary to understand how scope for production scales with size.

The relationship between body size and reproductive output and the drivers of this relationship are important to resolve, both from fundamental and applied perspectives. Fisheries models make strong and explicit assumptions about reproductive isometry and the scaling of energy intake. For example, `balanced harvesting’ practices are predicated on net production being relatively higher in smaller fish than larger fish [38]. Global climate change is driving down the body sizes across a wide variety of taxa – the impacts of these declines on population productivity depend in part on how reproduction scales with body size [21,38]. We have

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**Box 2. Why Does the Energy Density of Offspring Decrease with Maternal Size?**

In addition to showing that fecundity scales hyperallometrically with size, Barneche et al. [38] revealed systematic patterns in egg energy content across mothers of different sizes: larger mothers produced larger, but less energy-dense eggs than did smaller mothers. Overall, the relationship between maternal size and offspring size is steeper than the relationship between maternal size and offspring energy density. Larger mothers thus produce offspring that each have more energy in them in total. We have recognised that larger mothers produce larger offspring across a wide variety of taxa, with diverse theories to explain such patterns [81]. However, the finding that larger mothers produce larger and less energy-dense offspring is novel and, as far as we are aware, is unanticipated by theory. This finding directly contradicts the explicit assumptions of a suite of biphasic models and mechanistic theories of growth which assume constant energy density of reproductive components across the life cycle (Table S1). Furthermore, the majority of other life-history and mechanistic models of growth are silent with regards to ontogenetic changes in energy density of reproductive components, and thus implicitly assume that energy density is constant. It is difficult to explain this systematic and widespread change in energy composition of eggs across females of different sizes. A recent study showed larger eggs are more efficient at developing to the feeding stage [82] – perhaps because this increased efficiency allows larger eggs to be less energy dense. Future studies should determine whether other taxa show covariance between size and the energy density of offspring, and new theory should be developed to account for this covariance.
argued here that the longstanding and pervasive assumption of reproductive isometry is no longer supported by the data in a major group of animals and for a wide variety of other taxa. We suggest that this should cause us to re-evaluate how we model organismal growth (see Outstanding Questions).

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