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ORIGINAL ARTICLE

# August Pütter (1879–1929) and the Mechanistic Origins of the Temperature–Size Rule

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**Abstract**
One of the consequences of global warming is reduced final body sizes in animals of different orders, mainly in aquatic ectotherms like fish or water-breathing invertebrates. In this article, we identify August Pütter (1879–1929) as the originator of what is now called the "temperature–size rule" and as the first physiologist to develop a mechanistic explanation for this phenomenon. While Pütter's growth model was indirectly influential through its adaptation by Ludwig von Bertalanffy (1901–1972), his explanation of the influence of temperature on growth remained either unknown or misunderstood. In this contribution, we reconstruct the theoretical framework of his model and compare it to recent critiques of mechanistic models on growth and temperature. As we argue, Pütter's theory of "similarities of growth" provides explanations for observed temperature–size patterns trends that avoid later accounts of underlying "biological laws." While recent findings suggest that some aspects of Pütter's model need revision—for example, the proposed exponents of the anabolic and catabolic terms in his growth equation—we argue that his mechanistic model was designed in a way that could account for the multiple apparent exceptions to the temperature–size rule that were recently found.

**Keywords** Growth · History of biology · History of physiology · Mechanistic explanation · Temperature–size rule

## Introduction: Climate Change in the Mirror of "Rediscoveries"

One of the consequences of global warming is a reduction of final body sizes in animals of different orders, a trend that has been described as a consistent or even "universal" response to climate change (Gardner et al. 2011; Prokosch et al. 2019). While this phenomenon has been identified in organisms from all phyla, it is most prominent in water-breathing ectotherms such as fish, crustaceans, squid, and other mollusks (Cheung et al. 2013; Rubalcaba et al. 2020; Verberk et al. 2021). The consequences of this phenomenon are yet to be evaluated but since body size also predicts reproductive success of organisms with indeterminate growth, impacts on population stability are among the expected outcomes (Sheridan and Bickford 2011; Pauly and Cheung 2018; Audzijonyte et al. 2019). This trend has received increasing attention since it also affects fisheries and global food chains and its effects are already felt by the fishing industry (Cheung et al. 2021).

The causes and mechanisms behind this phenomenon are currently under debate and a number of different explanatory models have been proposed by ecologists and physiologists, some of which seem mutually exclusive (Audzijonyte et al. 2019; Pauly 2021). The phenomenon of temperature-induced changes in growth and final size is often referred to as the "temperature–size rule" a term coined by Atkinson (1994). While Atkinson briefly discussed earlier theoretical work on this phenomenon—for example, Ludwig von Bertalanffy's (1901–1972) discussion of growth and temperature—he was unaware of the origins of these theories. Von Bertalanffy's model of organic growth was largely adopted from German physiologist August Pütter (1879–1929), whose work received far less attention in the debate around growth and temperature.

More recently, Glazier (2018) has proposed to evaluate possible "rediscoveries" from earlier physiology to overcome current explanatory deadlocks in the debates around metabolic scaling, growth, and temperature. Older theoretical approaches to the question of size reduction and growth

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plasticity have received more attention since. In a recent review, Kearney (2021) discussed five different growth models and the role of temperature in each of them. Kearney identified Pütter as the originator of the temperature–size rule but despite the reintroduction of Pütter's work into the debate on growth and temperature in ectotherms, most of the literature that uses Pütter's growth model is unfamiliar with his original work on temperature and growth (Pütter 1911b; 1920). The problem with Pütter's reception is that his texts were seldom addressed directly and his ideas entered biological debates only through the work of von Bertalanffy, who incorporated Pütter's central ideas into his own theory (von Bertalanffy 1934; Bertalanffy 1951). As a result, Pütter's work was and still is rarely read and his growth model was only addressed on the basis of versions modified by others. Pütter's growth equation now underlies growth models in disciplines ranging from fisheries science, poultry farming, and agriculture to cancer research and epidemiology (Kühleitner et al. 2019; Brunner et al. 2021); and its growth model provides the foundation for the Dynamic Energy Budget Theory (Kooijman 2010), the Metabolic Theory of Ecology (Brown et al. 2004), and the Gill-Oxygen Limitation Theory (Pauly 2021). These newer theoretical approaches provided different mechanistic foundations for Pütter's model, and expanded its explanatory scope by discussing the relationship between growth and other traits (Kearney 2021). The most elaborate version of these theoretical expansions may be Kooijman's Dynamic Energy Budget (DEB) Theory (2010), whose model accounts for a wide range of physiological traits and their respective energetic expenditures. However, evaluations of what later became the von Bertalanffy or Pütter–von Bertalanffy growth model were seldom informed by Pütter's original work, which makes it worthwhile to connect newer insights into temperature–size relationships to a close reading of the original.

In this article, we reexamine Pütter's model on growth and temperature in the context of early 20th-century physiological theories and relate it to the current debate on fish growth and climate change. We show that despite the success of his growth equation through Bertalanffy's popularization, the mechanistic foundation of Pütter's model of temperature and growth has often been addressed superficially and sometimes prematurely dismissed, which probably also results from the fact that most of his work was never published in translation. The only text that is available in English is his 1920 essay on "Analogies of Growth," which circulated as a typewritten "preliminary translation" by Robert R. Parker (Pütter 1960) and was commissioned by the Fisheries Research Board of Canada. This draft translation, however, remained virtually uncited in the later literature and suffered from missing words and incomplete equations, while some of the key concepts were translated ambiguously (e.g., "Betriebsstoffwechsel" as "basal metabolism"). Although Pütter has been recognized in the international literature as the originator of the temperature–size rule a century later (Kearney 2021), a large portion of the current literature on temperature–size effects argues that the mechanistic explanation based on Pütter is inconsistent with empirical data (Atkinson 1994; Angilletta and Dunham 2003; Angilletta 2004). This view, however, is not directly based on the 1920 paper but on the adaptation of its growth model by others.

Our reevaluation of Pütter's identification of the "temperature–size rule" has two aims: first, it reintroduces Pütter's original temperature model into the current debate on temperature and growth. Even though some aspects of this model will undoubtedly need revision, a better understanding of its theoretical underpinning may be relevant to the contemporary debate. Second, we seek to shed light on theory formation in early 20th-century physiology and its quest for more general models. Going back to the original German texts (and discussing their most important concepts in the glossary), we first situate Pütter's metabolic theory in the context of physiological research of its time and relate it to ideas about metabolism and surface–volume relationships. We then provide a detailed discussion of Pütter's theoretical model and the contested relationship between anabolic and catabolic coefficients at different temperatures, and apply his model to findings from the recent literature on this topic. As we show, Pütter was not the first to conceptualize growth as the relationship between anabolic and catabolic processes and this idea was already developed in the work of Claude Bernard (1813–1878) and Herbert Spencer (1820–1903), and then adopted by Patrick Geddes (1854–1932) and John Arthur Thomson (1861–1933). However, none of those authors mathematized this model of growth or related it to temperature as Pütter did. Finally, we discuss Pütter's approach in the context of a shift from explicitly mechanistic descriptions to more rules-based accounts: while 19th- and early 20th-century physiologists and biologists tended to disseminate their findings in descriptions of specific mechanisms, later generations often tried to deduce more general patterns and "rules" (cf. Bergmann's rule, Rensch's rule, Cope's rule, etc.). It is telling that Pütter never referred to temperature-induced size reduction as a "rule" or "law" (just as Bergmann's rule was not formulated as a rule initially) and that such nomological generalizations emerged only later. Such mechanistic attempts to generalize at a larger scale are therefore instructive in the current debate about (neo-)mechanistic explanations and they offer models of how the recognition of generalized patterns might be possible without resorting to underlying nomologic structures (Glennan 2017). This position can be characterized as a middle ground between mechanistic and more law-based descriptions, which allowed Pütter to bridge generalizing and individualizing explanatory accounts.

It should be noted that our use of the term "mechanistic explanation" does not position Pütter on either side of the controversy between vitalists and mechanists in 19th- and early 20th-century biology. In our terminology, we follow Allen (2005), who pointed at the double meaning of "mechanism" in biology, and we briefly sketch Pütter's position in the vitalism/mechanism divide which involved more deep-seated philosophical assumptions on the autonomy of biological life as a separate sphere of causation. However, our characterization of Pütter's explanation of temperature–size relationships as "mechanistic" mainly serves to distinguish it from mere phenomenological descriptions which do not identify underlying causal explanations for the observed phenomena. In contrast to researchers who described these relationships as the "temperature–size rule" in the 1990s and later, Pütter's considerations start from an explanatory mechanism rather than from an identification of an omnipresent pattern (or "law" as Atkinson put it) for which a mechanism needs to be found yet. This mechanism-based description also allowed Pütter to explain the exceptions to the temperature–size rule that seem to puzzle recent accounts of this phenomenon (Audzijonyte et al. 2020). The relationship between mechanism and vitalism and the positions taken by Pütter and his collaborators will be briefly addressed in the next section.

## Pütter and the Quest for Physiological Theory

Pütter's seminal 1920 essay on "Similarities of Growth" ("Wachtumsähnlichkeiten") that contained the growth equation and laid the base for growth models in a wide variety of disciplines appeared as part of a series of papers on "physiological similarities," all published between 1917 and 1920. This series was not Pütter's first attempt to present a wider generalization of physiological processes: in 1911, he published his *Comparative Physiology* (*Vergleichende Physiologie*), a thoroughly theorized account of physiological phenomena across phyla and species (Pütter 1911b). While this work discusses growth and its reliance on metabolic processes in detail, it did not yet contain the classic growth equation of the 1920 essay that would later enter biological literature through von Bertalanffy's work. But even in his *Comparative Physiology*, the foundations of this growth model were already present, including the theory that described the impact of temperature on metabolism and growth (see p. 180).

Pütter's career fell into a period in which physiology was characterized by a renewed quest for theoretical generality and synthesis. In Germany, this development was still deeply informed by the legacy of Johannes Peter Müller, who was widely regarded the founder of comparative physiology. Major advances had been made in the decades after Müller's death, and new generations of researchers strove to provide unifying theoretical foundations for new findings and a comparative framework that allowed for generalizations across different phyla. Pütter, who was born in Stralsund in 1879, first studied zoology in Breslau (now Wroclaw) and graduated with a doctoral dissertation on the physiology of vision in aquatic mammals in 1901. In 1903, he went to Göttingen to earn a medical degree under the supervision of the famous physiologist Max Verworn with whom he collaborated for several years. Despite his prominent status in German physiology at the time, Verworn was in fact a highly idiosyncratic scientist and thinker. He explicitly positioned himself in the tradition of Müller and wrote a synthesis of modern physiology in 1894, titled *General Physiology* (*Allgemeine Physiologie*) but also published on divergent topics, ranging from archeology, philosophy—mainly epistemology—to art and psychology (Verworn 1901; Stang 2023). The introduction to his *General Physiology* contained a historical overview of the field and an epistemological critique of the human ability to know and comprehend natural processes. This somewhat idiosyncratic theory, which he later called "conditionism," dismissed attempts to causal explanation as the result of a human "causality instinct" ("Kausalitätstrieb," p. 34.) and instead called for an analysis of the conditions that enabled phenomena to occur (Stang 2023).

While Pütter was more reluctant to engage in such philosophical debates or in speculative experiments in other disciplines, he too was an unconventional scholar in many respects. As Würzburg physiologist Edgar Wöhlisch wrote in his eulogy, Pütter "embodied a type of scholar that is uncommon in the age of biological specialization: a theoretical polymath who strived for deeper natural-philosophical understanding beyond the countless individual findings" (Wöhlisch 1929, p. 692). During his lifetime, and as a professor in Kiel and Heidelberg, he was primarily known for his work on endocrinology, the physiology of vision, as well as a controversial theory on the nutritional sources of water animals, which he believed to be largely dependent on dissolved organic matter as a food source (Pütter 1911a). This theory was dismissed by many colleagues at the time, especially by August Krogh, but continues to be a topic of investigation until today (Jørgensen 1976; Wendt and Johnson 2006; Briée 2011). His mentor Verworn was one of the few colleagues who supported Pütter's idea on dissolved organic matter as an important food source for aquatic animals (Verworn 1909).

While the controversy between vitalists and mechanists had reached its height before Pütter started publishing, the environment in which he was trained, especially in Göttingen, was characterized by attempts to find a middle ground between speculative vitalist obscurantism and mechanistic reductionism. Pütter's mentor Verworn, for example, rejected reductionist mechanistic approaches, but was also careful not to be associated with vitalist accounts that assumed an occult life force behind organic processes (Verworn 1901, 1903). Pütter took a similar but slightly different approach: in his account, physiological processes as well as biological entities could best be explained from the perspective of organization of inanimate matter from which phenomena emerged that could not be reduced to their individual parts. In a 1915 essay on the question of how life could be defined, titled *"The Characteristics of Life"* ("Kennzeichen des Lebens"), he listed three features that distinguish biological life from inanimate processes: first, reproduction and metabolism, which he interestingly listed in the same category; second, irritability ("Erregbarkeit"), which became manifest in the ability to produce mechanical and electrical energy; and finally the integrity of functional structure (Pütter 1915). All these characteristics depended on an organization of different parts that created order through their mutual interactions, a perspective reminiscent of Immanuel Kant's famous distinction between organisms and physical mechanisms in the *Critique of Judgement* (Kant 1790).

In his later work, published during the 1920s, and especially in his introduction to physiology, titled *Steps of Life* (*Stufen des Lebens*), Pütter became more influenced by the so-called *Gestalt* theory proposed by Wolfgang Köhler and Max Wertheimer, and started to use the term *Gestalt*, or "configuration," to refer to biological entities like cells, organs, and organisms. Conceptualized as a "configuration," a cell should be understood as an entity that was "more than the sum of its parts" (Pütter 1923, p. 117) as it organized different processes and components in such a way that the parts and the whole were mutually dependent on each other. It was thus possible "to apply the concept of configuration on a cell as a living unit without running the risk of being accused of introducing a psychological or even mystical element into the realm of natural science by insisting on the concept of unity [*Einheit*]" (1923, p. 116). In this view, physiological processes relied on physics and chemistry but were not fully reducible to their underlying materiality because the interaction of physical and chemical elements and processes brought about a new configurational structure with distinct organizational principles. Even though Pütter identified this relationship between parts and wholes on different levels of organization from cells to organisms, his theory aligns with a strain of biological thinking that may be described as "organism-centered biology" and that took many different forms throughout the twentieth century (see Baedke 2019; Baedke and Fábregas-Tejeda 2023). Recent developments in theoretical biology and the philosophy of biology that build on such conceptual approaches are reflected in the current work of Michael Levin or the "theory of organisms" as proposed by Guiseppe Longo, Ana Soto, and others (see, e.g., Longo et al. 2015; Levin 2020).

## Surface-Volume Relationship in 19th- and 20th-Century Physiology and the Mechanistic Foundations of Pütter's Model

In the final chapter of his *Comparative Biology* from 1911, Pütter closed with a discussion of how and where nature showed similarities that could be detected and understood across taxa and phyla. These similarities were then expanded further in the aforementioned series of articles on "Physiological Similarities." As Pütter asserted, identifying similarities was the prerequisite to arrive at any form of generalizing theory in this field. Given this ambition to generalize across phyla, the scope of the 1920 essay and its new growth model was relatively modest insofar as it limited itself to the growth of aquatic animals only. In this model, growth was the result of two metabolic processes whose relationship determined the speed of growth as well as the maximum size an organism could reach: as Pütter stated, organisms did not stop growing because of the unavailability of additional materials that could be added to the system "but because the processes of buildup and breakdown reach an equilibrium" (Pütter 1920, p. 299). In this reasoning, breakdown was understood as the sum of processes that turn "a fully capable cell into a pile of rubble of disintegrating organic compounds" (1920, p. 299). At a certain point in an animal's life, these breakdown processes of cellular material outweighed the synthesis of new structures.

Conceptualizations of organismic growth that were based on the conflicting relationship between synthesis and breakdown were not entirely new and can be traced back to at least Jean-Baptiste Lamarck (1744–1829) As Lamarck pointed out, the growth of living and nonliving things was fundamentally different. While nonorganic objects can also grow—outwardly similar to organisms—this form of growth is of a different nature: crystals and minerals accumulate more substances and add them to their structure without any energetic costs, but living organisms also have to maintain the structures they have already built. These maintenance processes mainly involve "the repair activities which preserve it [the organism] during a limited time" (Lamarck 1797).

This view was further developed by Claude Bernard and Herbert Spencer. Spencer's *Principles of Biology* (1866) conceptualized growth as a result of the relationship between "surplus assimilation" and "expenditure." The balance between these two traits depended on the rate of resource supply and on body size and their relation to each other. Spencer's explanation of the relationships between these features was built on a surface-volume based model as discussed in the introduction and in more detail in the next section. Since resource uptake depended on surfaces which grew with a lower slope than the volume of the whole organism, isomorphic organisms had to invest an increasing fraction of their resource intake to replace what was broken down. Similar to Spencer, Claude Bernard described organismic life as the balance between the "synthesis" and the "analysis" of substances, where "analysis" stood for the breakdown of materials in the cell and the organism (see Bognon-Küss 2024).

Spencer's approach to understand growth was further developed by Patrick Geddes, a biologist and sociologist known mainly for his work on urban planning, and his colleague John Arthur Thomson. In their book *The Evolution of Sex* (1st edn. 1889), Geddes and Thomson further developed Spencer's theory and explicitly described growth as the balance between anabolism and catabolism and applied this model to both cells and whole organisms:

> The limit of growth, when waste has overtaken and is beginning to exceed the income or repair, corresponds in the same way to the maximum of katabolic preponderance consistent with life. The limit of growth is the end between anabolism and katabolism, the latter being the winner. (Geddes and Thomson 1889, p. 223)

While the idea that growth and size depended on the relationship between anabolic and breakdown processes in an organism's body already existed, Pütter was the first to mathematize this and to relate this mathematical model to observed size reductions at higher temperatures. The foundation of his reasoning was the following simple subtraction:

$$k \cdot \lambda^{2} - k' \cdot \lambda^{3} \tag{1}$$

Here, $\lambda$ represents the linear dimension that is proportional to the anabolic and the catabolic terms raised to the second and third power, and $k$ and $k'$ are the respective coefficients of synthesis and breakdown. This model presupposes that the anabolic term (synthesis) starts at a higher value (otherwise the organism would not be able to grow) but after a while, the catabolic term catches up more quickly and growth ceases when the two are equal.

Setting the exponents of the anabolic and catabolic terms to 2 and 3 implies a relationship between two different dimensions: since vital resources could only be absorbed by entering the system through a two-dimensional surface but had to supply a three-dimensional body, decreasing growth could then be explained as the result of decreasing resource supply capacities and the more rapid increase of the negative term with weight. While the 1920 paper did not indicate which specific surface limited the uptake of vital resources, the final pages of *Comparative Physiology* indicate that one central "physiological similarity" in organisms was the limit to growth and performance that was set by the capacity to take up oxygen (Pütter 1911a, p. 698). Echoing the German chemist Justus Liebig, Pütter argued there that the limit of an organism's performance was the "weakest link" in a chain of physiological processes: while there were animals for which the absorption of dissolved nutrients might set such a limit, for a wide range of phyla, the bottleneck was their capacity to absorb oxygen. This feature allowed for wider generalizations for the physiology of all those types of organisms "in whom oxygen consumption per surface unit reaches a value that is determined by physical properties, and thus marks an absolute capacity limit" (1911a, p. 698). In an earlier chapter of the book, Pütter presented elaborate calculations of the relationship between fish gills and the body mass they had to supply with oxygen, and in his 1909 study on dissolved organic matter, he showed that in scorpionfish or rock fish (*Scorpaena* sp.), gill surface area in juveniles was three times larger relative to body mass than in adults (Pütter 1911a, p.16). Such scaling effects between volume and surface informed Pütter's growth equation and the determination of the exponents of $\lambda$.

Surface-volume relationships played an important role in 19th-century physiological theories, and their relevance for biological processes can be traced back to Galilei's *Two New Sciences* (*Discorsi e dimostrazioni matematiche intorno a due nuove scienze*, 1638). Ratios between surface and volume have received the most attention in the context of Bergmann's rule, which explained thermal size clines and the trend to larger body sizes in colder climates through thermoregulatory adaptation. According to Carl Bergmann's famous essay, larger volumes relative to surface were advantageous as they minimized heat loss and thus reduced energy demand (Bergmann 1848; Pauly 2021). Even though a substantial body of literature applies the term "Bergmann's rule" to fish, amphibians, and reptiles, its originally proposed mechanism was only applicable to endotherms—the original essay from 1847 only discusses birds. Like Pütter's work, Bergmann was never fully translated into English and the debate about the proposed mechanism continues to be a topic of discussion even though the original makes clear that Bergmann's focus was not the identification of a general rule but of a mechanism that could explain a cline in size across many genera and families of birds; see, for example, Watt and Salewski (2011).

Earlier, Sarrus and Rameaux (1838), had examined oxygen consumption and heat production in vertebrates and identified a proportionality of respiratory and cardiac capacity. As the authors inferred, larger endotherms needed relatively less energy to maintain their body temperature (Sarrus and Rameaux 1838; Rubner 1893). A similar reasoning informed the work of Max Rubner in the 1880s and 90s and the so-called "surface law" that provided an explanation for metabolic scaling and the observation that larger endotherms consume relatively less energy compared to smaller ones (Rubner 1893).

Such theories, however, did not explain thermal size clines and temperature-induced growth plasticity in ectotherms, or the similarities between metabolic scaling relationships and surface-volume ratios. To explain these phenomena, Pütter's 1920 essay provided a different explanation by reasoning that the uptake of resources should depend on a surface through which the necessary substances entered the body, hence the scaling exponents 2 and 3, corresponding to the second and third dimensions. Even though thermoregulatory explanations did not apply to ectotherms in the same way as in birds and mammals, they were still subjected to similar geometrical constraints. Many researchers adopted these exponents (2 and 3), most notably von Bertalanffy, who assumed these values as characteristic for what he defined as "growth type 1," which constituted a form of growth that was dependent on surfaces, and typical for fish, mammals, and lamellibranchs. Von Bertalanffy based these values confirmed in his experiments on guppies; later work suggested that the proposed exponents were not universal: while smaller fish may indeed show scaling relationships that are similar to the second and the third power, larger and more active species show very different values (Clarke and Johnston 1999). In a more generalized form, and expressed by von Bertalanffy, the Pütter equation takes the form

$$\frac{dW}{dt} = \eta\, W^m - kW^n \tag{2}$$

where *dW/dt* is the rate of growth, *W* body mass, $\eta$ and *k* the coefficients, and *m* and *n* the exponents of the anabolic and the catabolic terms. For different values, the exponent *m* in Eq. (2) can define scaling relationships between the anabolic term and body mass and thus the mass-proportional breakdown (if $n=1$). In smaller species like guppies the values for *m* given by Pütter and von Bertalanffy ($m \approx 0.667$) could indeed be confirmed to be to be relatively close to 2/3, while the scaling exponent across fish species can vary between ca. 0.6 and 0.9, but is smaller than 1, except in larvae and other very young individuals (Pauly 2021).

## Temperature and its Impact on the Coefficients of Buildup and Breakdown

While his growth equation in this basic form accounted for the competition between two different types of energy expenditure, Pütter realized that its descriptive power depended on the correct determination of the coefficients of the anabolic and the catabolic terms (*k* and *k'* in Pütter or *H* and *k* in Pauly 2021). In comparisons between "colder" and "warmer" populations of the same species, animals in warmer environments first outgrow their conspecifics in colder regions but eventually remain smaller (Pütter 1920). As Pütter had already described in his *Comparative Physiology* from 1911, which neither contained a mathematization of these phenomena, nor a written growth equation, the anabolic term had a different temperature sensitivity than the catabolic term. In order to express the relationship between growth and temperature more specifically, Pütter first teased apart the properties of the anabolic term and then proposed an equation that can determine body size at a given time.

First, he defined the anabolic term as follows:

$$k = \frac{a\,p}{p+q} \tag{3}$$

Here, *p* stands for a diffusion coefficient (which depends on materials with "the properties of a membrane"; see Pütter 1920, p. 308), *a* is an equilibrium concentration of a chemical reaction that describes the respective concentrations at which the involved reactants are in equilibrium. *q* represents the temperature-dependent rate of energy metabolism and is thereby understood as a reaction constant, because Pütter assumed maintenance costs to increase exponentially with temperature. Note that in Pütter's work energy metabolism ("Betriebsstoffwechsel") is technically not identical to maintenance metabolism and only refers to those metabolic processes that provide energy, which can later be used for different expenditures, including growth and repair (see glossary). However, since the energetic consequences of both parameters are similar in relation to the anabolic term *k* and its components in Eq. (3), they can be used interchangeably in this context (for a discussion, see Pütter 1911b, pp. 119–120).

To illustrate the relationships between the components of *k* (*a*, *p*, and *q*), Pütter used the model of a water barrel with an in- and outflow to visualize the concentration of substances that are used in both growth and energy metabolism. The water level in the barrel is termed *x*, which is understood as equal to *k*. It represents the concentration of these substances and is directly governed by the in- and outflow. The inflow is dependent to the diffusion coefficient *p* and the equilibrium concentration *a*, which metaphorically represents the amount of water in the system, as water can only enter the container between the top of the barrel and the water surface. The outflow, $q$, however, which can be understood as an extensive parameter with regard to mass, is a measure for the substances that are needed to fuel energy metabolism and increases exponentially with temperature. The possible inflow of substances in an empty water barrel is larger than the substances used for energy metabolism, and the dynamic interaction between $p$ and $q$ determines the water level. As the barrel is filling up, the rate at which the water level rises will decrease—and eventually become zero—as the concentration of substances that are broken down and resynthesized are proportional to each other. A full water barrel would describe the biological situation in which the organism would be able to obtain the highest growth rate. If the inflow is reduced while maintenance metabolism continues, the water level will decrease again until the in- and outflow are the same: the organism stops growing if this equilibrium is obtained. Figure 1 depicts the water barrel schematically and can be used to illustrate the relationship between $p$ and $q$ for the respective sizes of an organism over time. Note that this metaphor is not unambiguous, as Pütter's verbal description explains the concentration of substances ($x$) that can be metabolized as "height," but does of course relate to a third dimension. The exact values of inflow and outflow and their dynamic relationship require a more specific definition (see below). The observation that the water level will first increase faster, and then gradually decrease, does not follow from the geometrical properties of the water container but from the mathematical model that underlies Eqs. (2) and (3).

Growth rates differ during the life history of an organism and, as Pütter argued, they are dependent on temperature in ectotherms. While $p$ increases linearly with temperature, the increase in $q$ should be exponential—Pütter estimated a value of $Q_{10}=2$. The term $a$ is then expected to be unaffected by temperature. Using a number of realistic values that $p$ and $q$ could possibly take, Pütter demonstrated that final sizes will be reduced in most scenarios (but not always, as we will discuss in the fifth section). He then used the following equation to express the final possible size of an organism, $L$, and its dependence on temperature:

$$L = \frac{k}{k'} \tag{4}$$

.

This implies that an organism's final size will typically increase at the lower ranges of the respective thermal optimum and decrease at the higher ranges, while growth rates will show an opposite trend in the early life-stages of the organism. Once a final size can be determined, length size at a given time can then be expressed as follows:

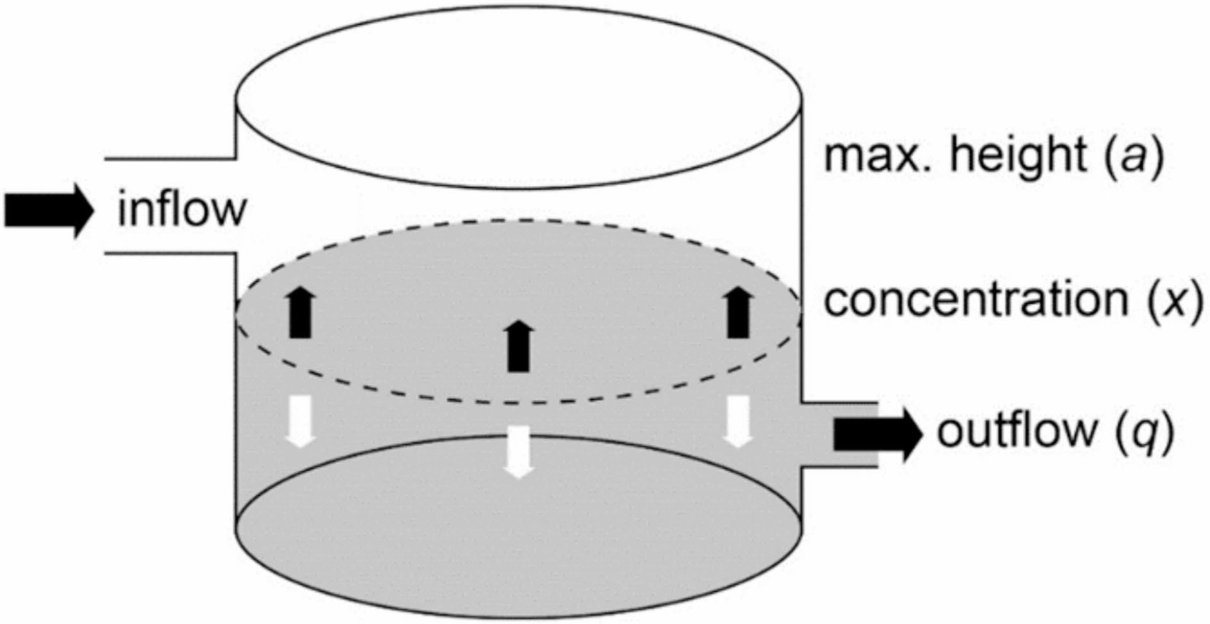

**Fig. 1** Water barrel model used in Pütter's "Similarities of Growth" (1920). Note that the concentration $x$ (which Pütter understood as interchangeable with the anabolic term $k$) represents a volume, not a height. The inflow is determined by the diffusion coefficient $p$ (which relates the squared linear dimension to time) and the maximum possible concentration $a$. The outflow (**a**) is proportional to the rate of energy metabolism, which increases exponentially with temperature.

$$\lambda = L\left(1 - \alpha\, e^{-\frac{c \cdot t}{L}}\right) \tag{5}$$

.

Here, λ is the length of the organism at a given time, $\alpha$ the constant of integration that corresponds to body length when $t = 0$ (which could always be at 1% of the respective animal's final size), and $c$ the growth coefficient, that indicates at which speed $L$ was reached. This equation was slightly modified by von Bertalanffy with $k$ as the growth coefficient and $t_0$ as the age at which the length of the organism would have been zero, which must then always be a slightly negative value:

$$l\,(t) = L\left(1 - e^{-K(t - t_0)}\right). \tag{6}$$

Even though Pütter's growth model allows for a phenomenologically accurate description of temperature–size effects as they are confirmed by older and newer data material, the model has been criticized on empirical grounds and with arguments that questioned its internal coherence. Already in the seminal paper that coined the term "temperature–size rule," the descriptive validity of the model was questioned (Atkinson 1994). According to Atkinson, the Pütter model (believed to originate from von Bertalanffy by the author) contained an inherent logical problem: if faster initial growth and final size reduction are a consequence of the different thermal sensitivities of the anabolic and catabolic terms, a decrease in maximum size would also result in declining growth rates. This reading of Eqs. (1) and (2) would be validated if the relationship between anabolic and the catabolic terms were constant over a given range of body sizes. This is not the case, as Eqs. (5) and (6) show. Equation (1) only represents growth at a given time in life-history and does not allow for inferences on the entire growth trajectory. Atkinson's argument was already countered by Perrin (1995), who pointed out that the relevant parameter was not growth rate over the entire life-history, but the growth coefficient that indicated the time in which asymptotic size, here $L$, was reached. This relationship between growth rate and coefficient is also illustrated by the fact that small fish species tend to have far higher growth coefficients than large ones, since it takes less time to reach a lower maximum size.

It is also important that Pütter's definition of the anabolic term, $k = a \cdot p/(p + q)$, where $p$ and $q$ react differently to temperature, does not predict a linear pattern that produces the same outcomes over a wide range of temperatures, but that it specifies the differential influences of the respective parameters. While Atkinson (1994, pp.18–19) concluded that the Pütter/von Bertalanffy model implied a linear increase of anabolism and an exponential increase of catabolism with temperature, this reading is not supported by Pütter's original model. Even before its mathematization in the 1920 paper, Pütter explicitly described the impact of temperature on protein synthesis (or anabolism) as peaking at a respective thermal optimum and then rapidly declining, for example in in his *Comparative Physiology* (Pütter 1911b, p. 180). Again, everything depends on the specific values of the parameters. As long as the initial value of $p$ is very low, the maximum size will first increase with rising temperatures and then quickly decrease. Only at higher values of $p$, body size will decrease immediately as temperature increases and the largest sizes are reached at the lowest temperatures within the range of thermal tolerance (depending on the value at which the diffusion coefficient $a$ is set). What follows is that Pütter's model does not assume a linear or constant relationship between temperature, growth, and body size. Instead, his mechanistic explanation acknowledges the possibility that specific temperatures can have specific and nonlinear effects on size and growth (see Fig. 2).

Another objection against Pütter's (or von Bertalanffy's) explanation of temperature–size relationships was raised by researchers who collected respirometry data to determine the impact of temperature on protein synthesis and breakdown. In two widely-cited papers from 2003 to 2004, Michael Angilletta and colleagues challenged Pütter's and von Bertalanffy's explanation of the temperature–size rule by referring to studies on different species in which the thermal sensitivities of the anabolic and catabolic coefficients seemingly differed from Pütter's predictions (Angilletta and Dunham 2003; Angilletta 2004). In many of the cited cases, growth efficiency did indeed increase with temperature—in some cases drastically—which indicated that the catabolic coefficient should indeed have a higher $Q_{10}$ than the catabolic term (Angilletta and Dunham 2003). However, as a closer look into the cited sources reveals, the cases in which temperature was reported to increase protein synthesis more than breakdown mainly relied on data on either juveniles or on tropical species with thermal preferences that were reached in the upper range of the experiments. This suggests that increasing growth efficiency with temperature may be a phenomenon that pertains to the first life stages of aquatic organisms, an observation that is in line with the fact that optimum growth temperatures consistently decrease with temperature in fish (Lindmark et al. 2022).

This observation is, however, already incorporated in Pütter's 1920 model. As he argued, his growth equation could not be used to model an organism's larval and early juvenile growth stages (as is the case with many mathematical growth models, including that of Pauly 2021). His reasoning was that the scaling relationships and geometrical proportions in larval organisms diverged significantly from those in larger juveniles and adults. As Pütter

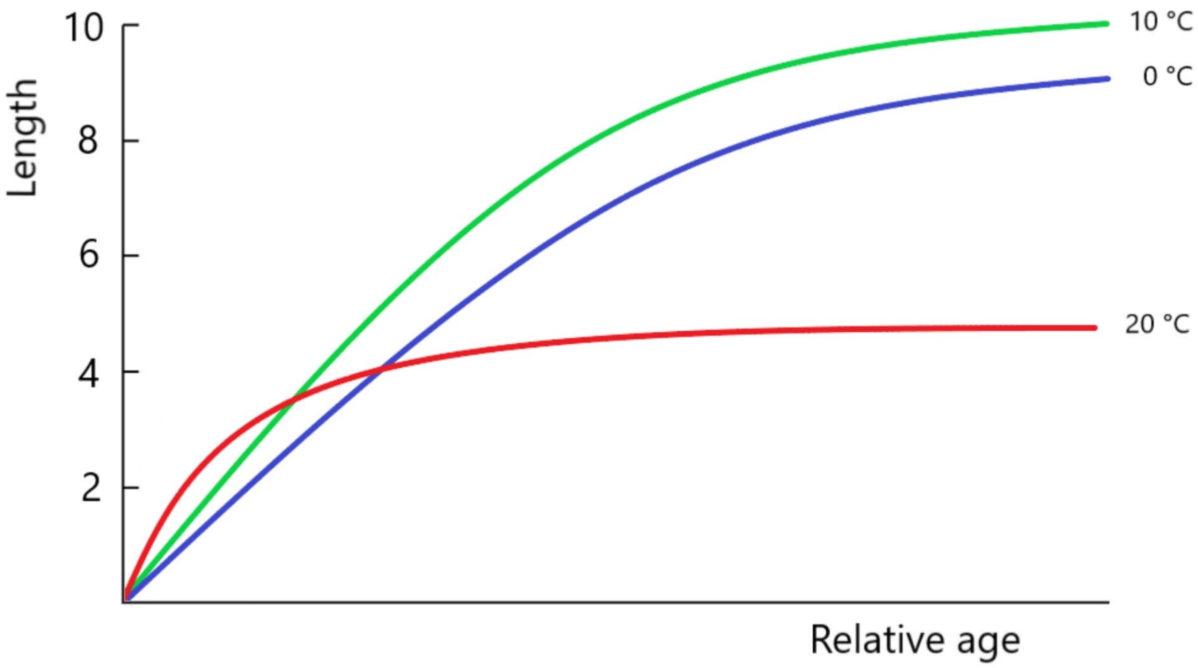

**Fig. 2** Growth curves of an undefined fish species at three different temperatures (adapted from fig. 1 in Pütter 1920). The respective growth curves are based on Eqs. (3) and (4) (with $p = 0.1$ and $q = 1$, which result in final size of 9.1 at 0 °C, 10 at 10 °C, and 4.6 at 20 °C). As this example shows, Pütter's model does not assume a decrease in final sizes with increasing temperatures in all scenarios and the species in this example grows larger at 10 °C than at 0 °C. Temperature–size effects depend on the values of p and q, as well as the respective temperature coefficient which is here assumed to be $Q_{10} = 2$. Note that Pütter noted neither the lengths nor the time units since these growth curves only serve to illustrate his model

stressed, mathematical growth equations could only reliably be applied to real organisms if their geometries did not change significantly during the growth trajectory that was measured or calculated (1920, p. 314). If we apply Pütter's underlying idea of surface-volume relationship to this question, both geometrical and size differences result in very different ratios in larvae and very young juveniles, especially in life stages when the growth of respiratory surfaces and body mass can grow with similar exponents. What follows is that at very small body sizes (at which the intensity of breakdown metabolism is proportional to synthesis in Pütter's model), the effect of a temperature-induced increase of the catabolic term has only limited effects. While the temperature sensitivity of growth should be expected to increase at a larger size (because larger organisms have to resynthesize more cellular material), this effect cannot yet be measured in larvae and young juveniles. As Verberk et al. (2021) put it, more recent research suggests that the "thermal dependency of net growth efficiency is itself size dependent." If Pütter's assertion is correct, this would be in line with the extensive body of literature that reports a universal decrease optimal growth temperatures with body size and age (see, e.g., Björnsson and Tryggvadóttir 1996; Verberk et al. 2021; Lindmark et al. 2022). While this does not necessarily establish the validity of his growth model, it shows that the criticisms do not directly pertain to Pütter's work in the original.

It is important to note that Pütter's interpretation of the catabolic term of the growth equation only involved the breakdown of materials that had already been synthesized by the organism ("arteigene Substanz"; Pütter 1920, p. 330) but not the breakdown of ingested nutrients which could then be used for the synthesis of new materials (which would be part of energy metabolism of "Betriebsstoffwechsel"). The above-mentioned "rubble pile" (Pütter 1920, p. 299) that was the result of these processes would inevitably increase with temperature, while the synthesis of new materials had to slow down at a certain thermal range. If breakdown is understood as the catabolism of ingested large molecules into smaller ones, the interpretation of Pütter's model may indeed result in different theoretical assumptions on the temperature sensitivity of both terms, and thus, of growth itself.

## Physiology and the Comparative Method

In his 1911 *Comparative Physiology*, Pütter proclaimed a separation between physiology and biology: the former could be conceived as a nomothetic science and the latter an idiographic discipline in the sense of Heinrich Rickert and Wilhelm Windelband, whose neo-Kantian philosophy used these concepts to distinguish between the sciences and the humanities. According to Rickert's and Windelband's model, the aim of the natural sciences was the identification of general patterns or law-like *nomoi* from which individual phenomena could be deduced. On the other hand, historical phenomena retained an individual and singular character that could not be explained by recurring to general laws. In Pütter's account, genuinely biological questions were in essence "historical" as they concerned the "becoming" of things (1911b, p. 1). Physiology, by contrast, tried to unravel the generality of natural processes and phenomena, and find their regularities. Attempts to formulate nomothetic principles in biology coincided with a trend towards increased mathematization, and both developments reflect the need that was felt at the time by many biologists to elevate their discipline to a field that could measure itself with chemistry or even physics (see, e.g., Morgan 1927).

According to von Bertalanffy, the identification of absolute "laws" and "exactly comprehensible regularities" was one of the main aims of a truly scientific physiology, an idea that shaped the program of his *Theoretical Biology* (1951, p. 14). Pütter's four essays on "Physiological Similarities," by contrast, rarely use the term "law" or "rule," and if they do, these terms refer to chemical or physical phenomena. However, as Pütter underlines in the introduction to the "Similarities of Growth" essay, his

> theoretical derivations are based on the principle that processes in living systems can only be based on assumptions that are confirmed in physics and chemistry and that can be determined in mathematical terms. So far, I have never found a reason to abandon this principle in any case. (Pütter 1920, p. 298)

The growth essay sheds a different light on Pütter's earlier discussion of the nomothetic and the idiographic sciences. Physics and chemistry provide the explanatory basis for biological reasoning. However, this does not necessarily imply that biology follows law-like principles per se, but that physics and chemistry constitute the constraints that define the boundaries in which biological processes can take place. This principle also informed his later idea of "configurations" in biology (Pütter 1923). As discussed above, biological configurations relied on the organization of physical and chemical structures through which new forms of order could emerge (see also Pütter 1915).

This reasoning not only goes beyond the divide between mechanism and vitalism whose aftermath still informed biological debates of the 1910s and 1920s but also illustrates Pütter's understanding of nomothetic principles in physiology. Nomothetic accounts understood in this way do not assume entailing laws that determine every aspect of physiological processes but rather reveal mechanisms that can be found across diverse phyla and produce similar outcomes. The concept of similarity is crucial in Pütter's entire work. In the introduction of the "Similarities of Growth" essay, he defines it as follows:

> Similarity is always "partial sameness," or sameness with regard to a specific feature or relationship. Finding these similarities is one of the great tasks of comparative physiology. Every awareness of a similarity in places where we first only saw differences brings us one step further on the way to a general physiology. (Pütter 1920, p. 298)

While Pütter was not a mechanist in the sense of the vitalism/mechanism divide, this approach justifies a characterization of his theoretical program as "mechanistic," in the sense that its explanatory foundations relied on mechanisms that produced certain effects or outcomes. These mechanisms could only be made visible by applying a comparative method whose aim was not so much the identification of universal laws but rather of casual relationships that produced similar effects in different organisms and situations. This comparative approach allowed for an elegant conceptualization of widely observable phenomena without relying on ad hoc explanations for instances where the expected pattern could not be detected or when apparent exceptions occurred. It is thus not surprising that Pütter avoided a description of the observed temperature–size pattern in terms of a "law": as Eq. (3) shows, the impact of temperature depends on the values of $p$, $q$, and $a$, which determine if increasing temperature will result in size reduction. However, these three values were not the only factor that informs the phenomenology of temperature-induced size plasticity. Referring to studies on clams and other invertebrates that produce large calcium carbonate structures, Pütter argued that these taxa showed different size clines: due to the fact that it was more difficult to build such structures in colder water, temperature-dependent size patterns in these organisms differed phenomenologically from other water-breathing animals, even if the same mechanism applied to them as well. Hence, clams could be larger in warmer water while temperature still had the same physiological effect, a prediction that could be confirmed for (tropical) giant clams of the genus *Tridacna* (see, e.g., Griffith and Klumpp 1996). The more recent postulate of the temperature–size rule as a "biological law for ectotherms" (Atkinson 1994) has produced a large number of exceptions, not only in terrestrial but also in aquatic organisms (Audzijonyte et al. 2020), a problem that was elegantly avoided in Pütter's approach to mechanistic explanation.

## Conclusion

Pütter's identification of the differential impact of temperature on the growth of aquatic ectotherms provides a number of relevant insights for the current debate around temperature-induced size reductions in fish and other organisms. Instead of referring to the observed pattern as a "biological law," his growth model identified a mechanism that predicts the specific impact of temperature on growth at different body sizes. Our analysis of his mechanistic model and its application to the recent debate about temperature-induced growth plasticity in ectotherms allows for the following conclusions:

1. Even though newer research has shown that Pütter's values for the scaling exponents of protein synthesis and breakdown metabolism need revision and that the exponent of anabolism is not universally 0.67 (but typically larger), his model offers a generalizing description of the current trend of body size reduction in aquatic ectotherms.
2. Studies that argued against the prediction of a lower temperature sensitivity of protein synthesis compared to breakdown metabolism were unaware of Pütter's original model (and Eq. (3)) in particular (Atkinson 1994; Angilletta and Dunham 2003; Angilletta 2004). Such studies leave Pütter's model untested as they primarily examined early life stages or tropical species with a limited thermal range. Tests of the thermal sensitivities of the respective coefficients should involve post-larval (and ideally adult) animals, since Pütter's model predicts differential effects of temperature at different body sizes (Angilletta and Dunham 2003; Angilletta 2004). While such tests sometimes indicated that Pütter's mechanism could only be confirmed within a small thermal range, it is important to consider the temperatures to which the species in question are adapted to develop a convincing experimental setup. While this leaves Pütter's hypothesis about the coefficients of anabolism and breakdown largely untested, recent studies about shifts in optimum growth temperatures at different body size lend support to Pütter's model (Lindmark et al. 2022).
3. While Pütter can be credited with the first identification of the temperature–size rule (74 years before Atkinson), his nuanced mechanistic model predicted temperature-induced growth plasticity at specific body sizes and temperatures. The recent problems with the numerous exceptions that occur when the temperature–size rule is understood as a "general biological law" (Atkinson 1994) did not occur in Pütter's mechanistic model that predicted differential effects of temperature and body size (see Eq. (3)).

Pütter's model illustrates a type of theory formation in early 20th-century physiology that aimed at generalizations in mechanistic terms in a period when the identification of rules or even "laws" started to inspire new approaches to biological modeling (Giere 1995; Cooper 1996). In this sense, Pütter's method of explaining patterns as a form of "similarity or partial sameness" (1920) aligns with more recent mechanistic models of explanations, as proposed by Machamer et al. (2000), Bechtel and Abrahamsen (2005), or Glennan (2017). This type of mechanistic explanation departs from references to larger nomologic structures under which local phenomena need to be subdued and instead it aims at the identification of specific mechanisms and causational interactions. While Pütter sought to help establish physiology as a nomothetic science, his approach to unravel general patterns reflected a way of biological theory formation that was more informed by a search for mechanistic structures as they were highlighted more recently. The underpinning of a generalizing growth model that could be applied across taxa and phyla illustrates how such approaches depended on local mechanisms that needed to be identified and theorized as factors that produced "similarity in places where we first only saw differences" (Pütter 1920).

## Glossary of the Most Important Metabolic Concepts in Pütter (1920)

- <u>*Aufbau*</u> ("buildup") => see *Baustoffwechsel*.
- <u>*Abbau*</u> ("breakdown"), often translated as "catabolism" in later publications, refers to the breakdown of organismic material, or the sum of all the processes that turn "a fully capable cell into a pile of rubble of disintegrating organic compounds" (1920, p. 299). *Abbau* ("breakdown") requires constant repair, which is carried out by processes that are part of buildup metabolism (*Baustoffwechsel*). Note that *Abbau* does not include catabolic processes of ingested food, whose molecules are broken down into smaller units.
- <u>*Abnutzungsstoffwechsel*</u> ("wear and tear metabolism") can be understood as "breakdown" (*Abbau*) but in certain passages (see, e.g., 1920, p. 336) it is also used in such a way that repair activities to compensate for breakdown are included (which is not surprising, given that breakdown and repair are proportional as long as an organism is able to maintain itself). The term is derived from Rubner's *Abnutzungsquote* ("rate of wear

and tear") and is also discussed in the context of ageing (Pütter 1920, pp. 307–310).

- *Baustoffwechsel* ("buildup metabolism") refers to the use of assimilated substances that are invested in the formation of new organismic materials. As Pütter explains in *Vergleichende Physiologie* (1911b, pp. 119–120), the term is not unambiguous and cannot always clearly be separated from energy metabolism (*Betriebsstoffwechsel*), which provides energy for a wide range of processes and can be invested in physical activity, maintenance or growth (see also Pütter 1923, pp. 143–147).
- *Betriebsstoffwechsel* ("energy metabolism") refers to the sum of all metabolic processes that produce energy that can then be invested in different energetic expenditures. In certain passages of the 1920essay (e.g., on pp. 300–301), Pütter uses *Betriebsstoffwechsel* in such a way that costs of growth are excluded and thus distinguished from buildup metabolism. In these passages, *Betriebsstoffwechsel* may better be understood as "maintenance metabolism" (indicating all expenditures except growth).
- *Wachstumsstoffwechsel* ("growth metabolism") refers to the portion of energy metabolism (*Betriebsstoffwechsel*) whose products are invested in the formation of new organismic materials. While buildup metabolism (*Baustoffwechsel*) is also used to pay for maintenance expenditures in non-growing organisms (by replacing materials that have been destroyed earlier), "growth metabolism" only refers to the metabolic expenditures associated with materials that do not replace lost substances.

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## Declarations

**Competing Interests** The authors declare no competing interest.

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