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Review

Developing animals flout prominent assumptions of ecological physiology

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Abstract

Every field of biology has its assumptions, but when they grow to be dogma, they can become constraining. This essay presents data-based challenges to several prominent assumptions of developmental physiologists. The ubiquity of allometry is such an assumption, yet animal development is characterized by rate changes that are counter to allometric predictions. Physiological complexity is assumed to increase with development, but examples are provided showing that complexity can be greatest at intermediate developmental stages. It is assumed that organs have functional equivalency in embryos and adults, yet embryonic structures can have quite different functions than inferred from adults. Another assumption challenged is the duality of neural control (typically sympathetic and parasympathetic), since one of these two regulatory mechanisms typically considerably precedes in development the appearance of the other. A final assumption challenged is the notion that divergent phylogeny creates divergent physiologies in embryos just as in adults, when in fact early in development disparate vertebrate taxa show great quantitative as well as qualitative similarity. Collectively, the inappropriateness of these prominent assumptions based on adult studies suggests that investigation of embryos, larvae and fetuses be conducted with appreciation for their potentially unique physiologies.
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Contents

1. Introduction

Every field of biology has its assumptions, tenets or doctrines. A set of beliefs, often repeated over generations of students, provides continuity as well as a comfortable

framework for interpretation of results and the planning of future experiments. Yet, when assumptions grow to become dogma, they can also be constraining and even lead us to overlook the most obvious contradictions embedded in familiar data. This essay will lead data-based challenges to several prominent assumptions, primarily in the area of physiology. These assumptions may have served us reasonably well in the context of the physiology

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of adult animals, but are proving less helpful in promoting our understanding of the physiology developing animals. These assumptions, which do not comprise an exhaustive list, are:

- Allometry features prominently as an overarching assumption in developmental physiology. This statement is rationalized by the seemingly ubiquitous role of allometry in the physiology of adult animals based on interspecific comparisons (e.g., Schmidt-Nielsen, 1984; Calder, 1984; Brown and West, 2000). Yet, the concept of allometry has historically been readily extended without verification to intraspecific comparisons of developing animals increasing in mass, a situation quite distinct from comparing different sized adult animals (e.g., Gould, 1966; German and Meyers, 1989; Klingenberg, 1998; Stern and Emlen, 1999; Koehl, 2000).
- Complexity increases progressively with development, especially in physiological systems. Organismal complexity has traditionally been measured by tracking increases in number, types and sizes of cells, tissues and organs (e.g., McMahon and Bonner, 1983), thus giving rise to a common view that complexity increases progressively (and even linearly) as animals simultaneously grow in size and maturity. Less attention has been paid to the interactions that might occur between structures (but see Bullock, 1993, 1999; Burggren and Monticino, submitted for publication).
- Functional equivalency occurs in embryonic and adult structures. Few would question the notion that the heart, kidneys or gut of immature animals function in the developing animal just as in the mature animal. Yet, such functional equivalency across all developmental stages of a species has rarely been questioned and consequently goes unsubstantiated by investigation.
- Duality of physiological control provides offsetting regulatory influences. Regulatory systems of adults often operate through the interplay of physiological inhibition and excitation. However, antagonistic systems do not appear simultaneously in developing birds, for example (Burggren and Crossley, 2002), suggesting that regulation in developing animals may operate under a different set of constraints and limitations.
- Phylogeny dictates physiology in embryos just as in adults. The wide range of adult physiological mechanisms and adaptations in vertebrates reflect similarly wide variation in adult morphology of highly disparate taxa. Nonetheless, most vertebrates share a similar vertebrate body plan, and in addition there is often unappreciated physiological similarity in early developmental stages comprising "the vertebrate embryo".

By showing that these assumptions regarding physiological development can be belied by the facts, it is anticipated that future experiments in developmental physiology will approach embryos, larvae and fetuses with a more sophisticated and, ultimately, more revealing set of guiding principles.

Let us know consider each of the assumptions listed above, in turn.

2. Assumption: developing animals follow principles of allometry

One of the most challenging aspects of understanding the physiology of developing animals is how to deal with allometry or scaling. Early developmental stages are typical not only immature, but small, whereas the late developmental stages are both mature and large. When we observe, for example, a change in heart rate during development of a fish, is it attributable to organogenesis or "simply" due to changes in body mass? To answer this question, let us consider allometry in more detail.

Allometry describes the change in proportion of similar shaped objects as a consequence of changes in their size. Allometry influences almost everything surrounding us— the change in proportion of nails as they get longer, the difference in construction of stringed instruments from violins to double basses, the alterations in ship construction as hull displacement increase. Allometry also pervades the biological world, where many relationships can be described by the allometric equation, $Y = aX^b$, where y is the variable of interest, x is the body mass and b is the allometric constant. Typically, b is ~ 0.75, so the variable of interest increases more slowly than body mass, yielding the familiar "mouse to elephant curve". Allometry is probably best known for metabolism but also applies to a whole host of biological features such as cell size, mitochondrial density, coronary vascular branching, circadian rhythms, brain mass, life span, arterial tree structure, hemoglobin oxygen binding, bone strength, etc. (see McMahon and Bonner, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Klingenberg, 1998; Stern and Emlen, 1999; Brown and West, 2000; Porter, 2001).

Interspecific allometry, where small adults are compared and contrasted with large adults, comprises the vast majority of allometric studies. Far less understood is intraspecific allometry—those changes that occur within an individual during its development and growth. Do physiological variables follow allometric growth during development?

Heart rate is an easily measured variable (though "easy" is a relative term when dealing with embryos, larvae or fetuses). Heart rate patterns during development have been reported for a wide variety of vertebrate species (Burggren and Warburton, 1994). While there is not single, dominating pattern, a typical finding is that heart rate increases sharply from the onset of heart rate, even as body mass increases. In the zebrafish, *Danio rerio*, heart rate increases from about 130 beats/min to nearly 190 beats/min during the first 20 days of development, even as body mass increases fivefold (Fig. 1). A qualitatively similar pattern occurs in amphib-
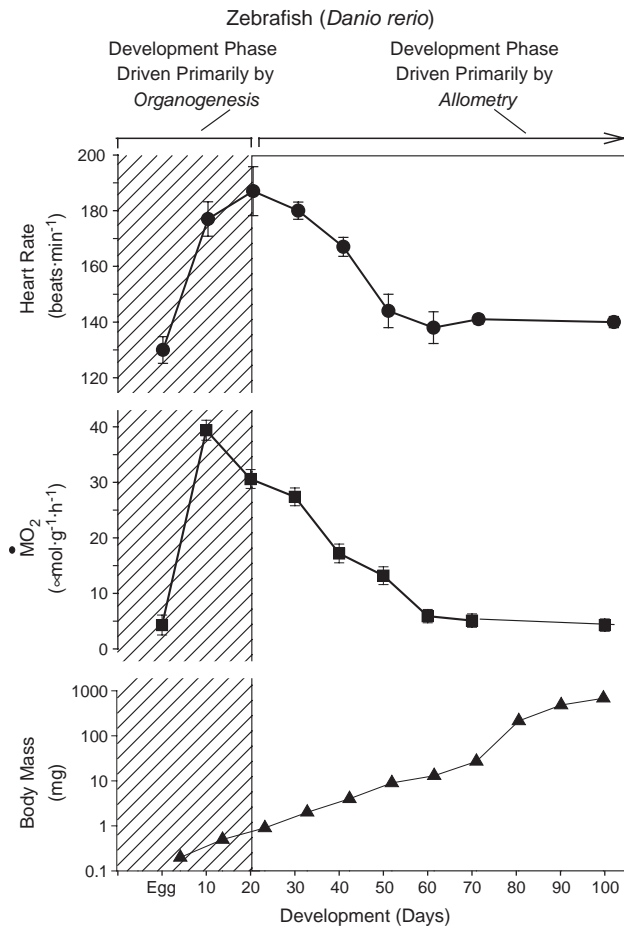
Fig. 1. Heart rate and oxygen consumption (28 °C) in the developing zebrafish, *Danio rerio*. Note how the earliest phases of development show an increase in physiological rates even as body mass increases, contrary to allometric predictions (after Barrionuevo and Burggren, 1999).

ians, reptiles, birds and mammals (see references in Burggren and Warburton, 1994; Burggren and Keller, 1997). The domestic mouse, *Mus musculus*, presents an interesting variation on this theme (Hou and Burggren, 1989). From birth to weaning, heart rate in the mouse increases even as body mass increases, completely counter to allometric predictions. From weaning to adulthood, however, heart rate declines with increasing body mass in a pattern predicted from simple allometric equations.

During early development, oxygen consumption like heart rate, shows patterns of change that are not easily explained by allometry. Returning again to the zebrafish, oxygen consumption shows a sharp increase in early development up until Day 10 concomitant with an increase in body mass (contrary to allometry), before eventually conforming to allometric predictions after Day 20 (Fig. 1). Similar patterns of increasing metabolic rate even as body mass increases have been reported in developing fishes (e.g., Rombough and Moroz, 1997; Bagatto et al., 2001; Green, 2004) and amphibians (see Burggren and Just, 1992 for review of earlier literature; Hastings and Burggren, 1995). Even different components of a developing animal

may act differently. For example, in the chicken *Gallus gallus*, the embryonic membranes (larger than the embryo in very early development) show the metabolic pattern mentioned above, while the embryo itself appears to follow a more conventional allometric pattern of metabolism during development (Romanoff, 1967).

Collectively, these data suggest that physiological processes (or at least two very fundamental processes—circulation and oxygen consumption) show an early developmental phase driven by the events of organogenesis, followed by a later developmental phase in which allometric relationships appear to "kick in". These hypothetical phases are shown Fig. 1 for the zebrafish, but can be similarly identified for numerous other species.

The apparent widespread flouting by developing animals of the tenet of allometry begs the question "Does the concept of allometry even apply to developing animals?" A fundamental allometric tenet is that different sized animals should be compared in the same physiological state. Yet, a fundamental developmental tenet is that physiological state changes dramatically with organogenesis and somatic growth. That these two tenets seem completely valid within their respective domains, yet are internally inconsistent when looking at a growing, developing animal, suggests that our understanding of the impact of body change during development (and, indeed, the impact of development on body mass changes), requires additional refinement. Specifically, we need to develop hypotheses that help validate and test emerging ontogenetic–allometric theories and models (Klingenberg, 1998, 2002; Hunt von Herbing, in press). Moreover, just as comparative physiology adopted a new suite of statistical tools to address multi-species comparisons (Garland and Adolph, 1994), developmental physiologists should be encouraged to work with applied mathematicians to develop statistical methodologies that enable allometric analysis concurrent with changes in physiological state.

3. Assumption: complexity increases with development

One of the most basic assumptions of developmental physiology is that complexity increases as development proceeds. Doubtlessly the physiological processes evident in a late stage bird embryo or a fifth instar decapod crustacean are far in advance of anything that occurs in early embryos when tissue differentiation and organogenesis predominate. However, two corollaries of this assumption about development and complexity are well worn yet not always valid. The first corollary is that complexity increases somewhat linearly during development. That is, an animal about half way through its development is about one half as complex as a completely developed animal. The second corollary is that the terminal, sexually mature stage of an animal is the most complex form.

While these corollaries form useful guiding principles, they fail us on numerous levels. First, viewing complexity as progressively increasing during development steers us from actively looking for complexity in early forms where we "…Know we won't find it". Thus, we may not focus physiological examination on earlier stages, since we erroneously conclude that such stages are not capable of complex physiological processes or control systems. Yet, there are manifold examples where physiological processes are most complex in intermediate stages. While this notion will be explored in more detail below, consider a familiar example. In the weeks prior to birth, your cardiovascular system was at its most complex structurally, in terms of the numbers of vessels and the number of alternate pathways for blood flow. Within a few minutes of birth, however, your cardiovascular system was shedding complexity with the closure of numerous vessels, shunt options, and or other blood pathways (e.g., closing of ductus arteriosus, ductus venosus, umbilical vein, umbilical artery, foramen ovale in the heart). While there is certainly much maturation of cardiovascular process to follow birth, from the perspective of pathways for blood flow, the post-natal form presents a simpler system.

A second way in which the assumption that complexity progressively increase with development fails physiologists is when we tend to make evolutionary arguments based on observations of *adults* rather than observations based on the ontogenetic sequence that comprises a species. Natural selection occurs at all development stages (e.g., Langille and Hall, 1989; Burggren, 1992; Richardson, 1999; Goldstein, 2001; Sly et al., 2003), and we risk skewed if not incorrect interpretations of our data if we fail to take into account the physiological processes in all developmental stages of an animal.

Part of the bias towards assuming adults are more complex derives from our relatively loose and casual use of the term "complexity". How do we actually analyze, measure and report the complexity of physiological systems? One approach to assessing complexity could be to consider an interplay of animal size, cell number and cell types (McMahon and Bonner, 1983). Thus, organisms such as redwood trees or blue whales are viewed as "more complex" not just because of size, but because they exhibit greater cellular differentiation into multiple cell types, which correspondingly allows more tissue types. This approach, which might be termed the "structural" approach to addressing complexity, essential counts parts, components or structures, and then equates the resulting sum to a measure complexity. A related approach that still involves counting "structures" might be to count the number of genes and the number of expressed proteins or their concentrations or their possible suite of actions. However, complexity also involves the number of physiological processes that flow from these structures or, at the molecular level, flows from proteins expressed by genes. Counting the number of ongoing processes – a methodology equally

simplistic as counting structures – yields a different but no more informative measure of complexity. However, both of these approaches to measure complexity ignore the interactions between structure (at any or all levels) and the physiology that derives from them. Indeed, taking into consideration such interactions provides a more sophisticated view of complexity than either approach by itself (Burggren, in press; Burggren and Monticino, submitted for publication).

The interaction of structures and processes as they contribute to complexity can be illustrated by considering the development of an anuran amphibian (more specifically, a terrestrial toad) from an aquatic larva to a terrestrial toad. In the first 10% of larval development, the newly hatched tadpole primarily uses skin in strictly aquatic respiration (Fig. 2A). Gills are quickly added, though all respiration remains still aquatic through approximately 2/3 of larval growth. As the tadpole develops and begins to use lungs during the last third of development, the numbers of respiratory structures and the types of breathing processes (water breathing, air breathing) both increase. With metamorphosis to the terrestrial adult, the great majority of gas exchange (at least oxygen uptake) is now achieved through pulmonary ventilation. Fig. 2B illustrates schematically how the numbers of respiratory structures and respiratory processes increase. If we consider the maximum number of interactions between structures and processes (i.e., number of structures X number of process), then we see that the hypothetical number of interactions is greatest in late larval development just prior to metamorphosis. Thus, both a structural and physiological perspective underestimate the true complexity compared to an "interactive" view of complexity that looks at the number of possible interactions between structures and processes.

Not reflected in the "interactive" view of complexity depicted in Fig. 2C is the fact that not all interactions between structures and processes are possible or desirable. In the example of amphibian development, interactions of lungs with water or gills with air are theoretically possible interactions, but not ones that realistically should factor into the assessment of complexity of respiration in developing anurans. Thus, as physiologists, we need to develop a more sophisticated set of statistical tools, mathematical approaches, and modeling procedures to accurately analyze physiological complexity in not only developing animals, but also in comparisons of different taxa or populations. Fortunately, applied mathematicians, computer scientists, material scientists, and other are very actively exploring the analysis of complexity with the goal of providing such direction (see Burggren, in press). However, mathematical perspectives and physiological perspectives do not always map onto each other. For example, a mathematician classifies a system as simple or complex based on whether the emergent behavior from that system is simple or complex. Yet, a physiologist knows that a very simple emergent behavior (e.g., a constant body
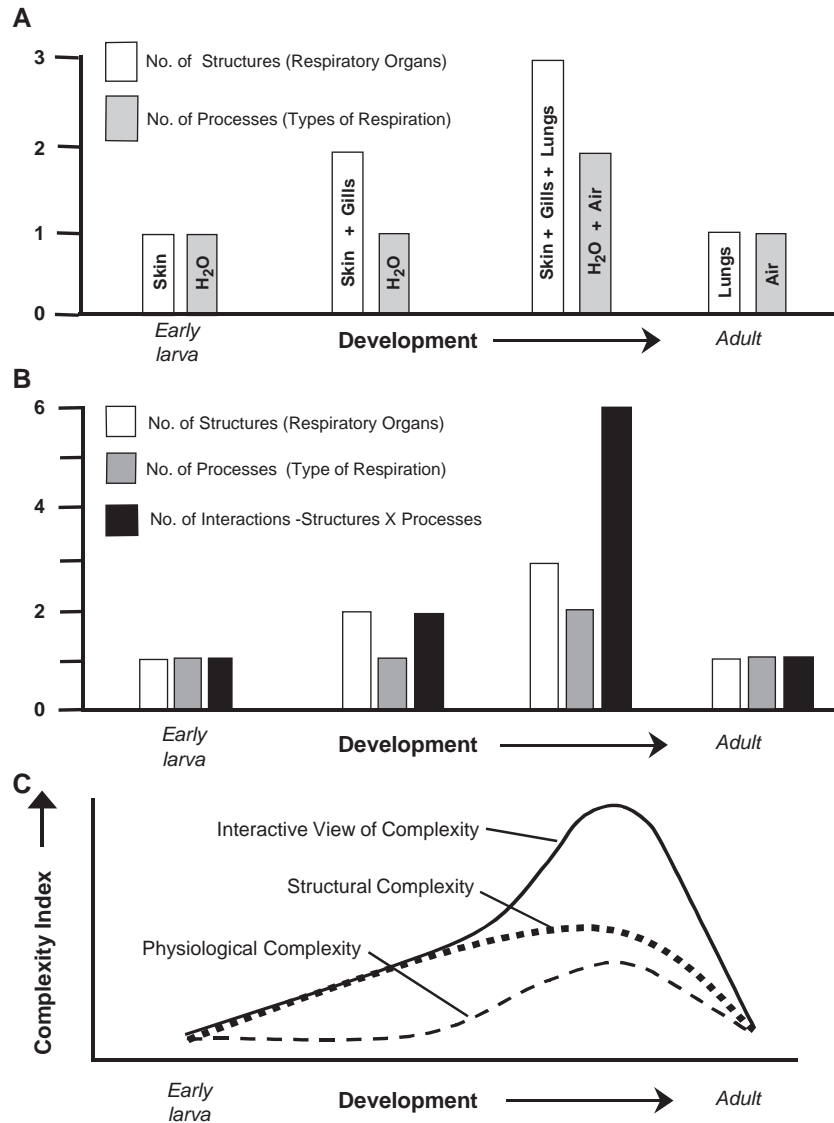
Fig. 2. Transformations in structural, physiological and "combined" complexity during the developmental transition of an anuran amphibian from an aquatic larva to a terrestrial adult. (A) Typical changes in the number of structures (respiratory organs) and processes (aquatic or aerial respiration) during development, as typically measured in an anuran such as the bullfrog, *Rana catesbeiana* (see Burggren and Just, 1992). (B) A comparison of complexity as reflected by the number of structures, the number of processes and the resultant number of interactions. (C) The interactive view of complexity, derived from panel (B), shows that respiratory complexity peaks in late development before falling in the adult.

temperature in a mammal of 37 °C) is the result of a very complex thermoregulatory system. Thus the physiological perspective conflicts with basic mathematical constructs. Despite these difficulties, our understanding of physiological complexity will likely move forward more rapidly through interactions with applied mathematicians with biological experience.

4. Assumption: embryonic and adult organs have similar functions

When, as physiologists, we look at an embryo, larva, or fetus, we subconsciously import myriad assumptions based on our knowledge of adult physiology. We see eyes, and

assume that rhodopsin is being bleached by photons to form opsin. We see myotomes and assume that their contraction is being activated by cholinergic postsynaptic receptors. We see kidneys and assume that they are ultrafiltering. Perhaps, most obviously, we see the beating heart and assume it is transporting oxygen and nutrients. Many of these assumptions are, of course, entirely valid, and we are safe by "playing the percentages". Yet, many such assumptions for developing animals are not only untested, but when tested prove to be simplistic at best, or completely incorrect at worst. Why do we make such assumptions? One reason may be that morphology and physiology are often viewed as tightly linked: that is, function flows from form. Yet, subtle changes in structure can lead to major changes in function (Burggren and Bemis, 1990). Nowhere does this seem more

evident than in the organ and organ systems of embryos, where evidence is gathering that suggests that embryonic functions of tissues and organs may have modified – even quite different – roles in embryos, larvae or fetuses compared with adults forms.

Perhaps best documented in this regard is our emerging understanding of the embryonic heart. Experimental approaches have employed heartless mutants of salamanders (Lemanski et al., 1995) or zebrafish (Stainier, 2001), surgical removal of presumptive heart tissue in salamanders (Kemp, 1953; Mellish et al., 1994; Grunz, 1999), disruption of blood oxygen transport in embryos of chickens (Cirotto and Arangi, 1989) or zebrafish (Pelster and Burggren, 1996) and obstruction of the ventricular outflow tract of chicken embryos (Burggren et al., 2000, 2004). Collectively, these studies reveal that normal tissue growth and metabolism can proceed independent of tissue perfusion in the early vertebrate embryo (e.g., 96-h zebrafish embryo, or 3- to 5-day-old chicken embryo), with effective oxygen and nutrient delivery and carbon dioxide and wastes being eliminated by the process of diffusion, alone. Thus, from the perspective of having to provide necessary material transport, the heart of many vertebrates appears to begin to beat and generate convective blood flow hours or days earlier than necessary, a phenomenon that has been termed "prosynchronotropy" (Burggren and Territo, 1995; Territo and Burggren, 1998; Burggren, 2004). While definitive experiments remain to be performed, we hypothesize that earliest function of the developing embryonic heart of vertebrates involves angiogenesis, rather than bulk transport. Vertebrate endothelial cells proliferate through the paracrine effects when shear-strain stress on them result in their secreting VEGF and other growth factors such as fibroblast growth factor (FGF-2), transforming growth factor (TGFβ1), ephrin and integrins (Tomanek and Ratajska, 1997; Zheng et al., 2001; Ferrara et al., 2003; Vargesson, 2003). We propose that early in development, the vertebrate heart generates pulsatility of blood and produces sheer-strain within the interior of the forming, endothelial lined. These stresses promote hormonal stimulation of angiogenesis, especially in the periphery (see Burggren, 2004). Others have suggested that prosynchronotropy in Teleost fishes might be involved in osmoregulation, or nutrient or waste transport (e.g., Kranenbarg et al., 2000; Rombough, 2002), though the same evidence that suggest bulk transport of oxygen is unnecessary in early embryos would seemingly hold for bulk transport of ions, water, nutrients or wastes. Prosynchronotropy is likely to be a general vertebrate trait, as it has been identified in fishes (Pelster and Burggren, 1996; Kranenbarg et al., 2000), amphibians (Territo and Burggren, 1998) and birds (Burggren et al., 2000, 2004).

Another example of an organ that changes function during development is the skin of fishes and amphibians. Very early in development of many larval fishes, the skin is the sole organ for gas and ion exchange (McDonald and McMahon, 1977; Rombough and Ure, 1991; Wells and Pinder, 1996; Rombough and Moroz, 1997; Rombough, 1997, 1998). Emphasizing the role of the skin in gas exchange, the larva of the air-breathing teleost fish *Monopterus* has have an elaborate counter-current cutaneous gas exchange system, with blood in cutaneous vessels flowing counter to the direction of water currents over the body surface generated by the pectoral fins (Liem, 1981). As the gills of growing larval fishes proliferate and take over as the primary site for both gas exchange and osmoregulatory exchange, the skin's function simplifies to serve primarily protective roles, and in many fish species becomes relatively scaled and less permeable to gases. Thus, whether we view skin as an important exchange site or merely a protective cuticle is largely a function of the animal's developmental stage.

As a final example of how embryonic structures may carry out modified or even entirely different roles in early developmental stages compared with the adult, consider the gut of anuran amphibians such as Ranid frogs or Bufonid toads. While the larvae of salamanders are strictly carnivorous, almost all anurans are herbivores (Larsen, 1992). This feeding style is reflected in the structure of the anuran gut, which is long, coiled and of high surface area, typical of all herbivorous vertebrates. As the larva approaches metamorphosis into a typically carnivorous adult, the gut begins to change radically. It decreases in length and develops the capability of pepsin secretion for the digestion of ingested animal tissue. Yet, largely unstudied are the attendant developmental changes in many aspects of its endocrine function of the gut and its secretory organs and tissues. In this respect, studying the alimentary system of the larva to gain insights into the adult – or vice versa – could be quite misleading.

Clearly, there are numerous, important examples of how the function of embryonic or larval structures may vary in highly significant ways from that of later developmental stages or the adult. Particular caution should be taken when extrapolating early developmental performance to that of the adult, or interpolating adult performance to explain early developmental phenomena.

5. Assumption: organs under dual physiological control

One of the basic assumptions of physiological regulation is the interaction between stimulation and inhibition, with the resulting rate typically reflecting the integration of these external influences. In vertebrates, system homeostasis in the short term relies upon an offsetting interplay between sympathetic and parasympathetic neural input. Whether stimulation results from synaptic release of catecholamines or acetylcholine, most every organ receives dual sympathetic and parasympathetic innervation. Indeed, the prevailing performance of an tissue or organ at any given time is the result of the "battle of the tones" between sympathetic

and parasympathetic input. A classic example is that of heart rate, which represents the balance between a stimulating cardiac sympathetic tone and an inhibiting vagal parasympathetic tone. Treatment with atropine or other cholinergic blockers will typically result in an increase in heart rate, revealing a parasympathetic vagal tone, while treatment with a β-blocker will decrease heart rate, revealing a sympathetic tone. While the specific effects of the sympathetic and parasympathetic nervous systems are highly specific to tissues and organs, the duality of sympathetic and parasympathetic control is nearly ubiquitous in physiological regulation in adult vertebrates.

Is this physiological regulatory duality as prominent in developing vertebrates? Studies of the ontogeny of key elements of cardiovascular and respiratory reflex control in a common model for development, the bird embryo. While dual regulatory mechanisms are the end-product of development, the earlier formative stages are characterized by highly asynchronous developmental onset of sympathetic and parasympathetic regulation. For example, in the chicken embryo, the onset of vagal control of the heart has variously been reported to first appear on Day 13 of incubation and subsequently strengthen for several days (Chiba et al., 2004) or to not appear until hatching (Crossley and Altimiras, 2000). Irrespective of when in late incubation full vagal control develops, adrenergic sympathetic cardiac control is in place by Day 12—well in advance of vagal control (Crossley and Altimiras, 2000). Interestingly, in the Muscovy duck, a contrasting pattern occurs where parasympathetic control of the heart substantially precedes sympathetic control, the latter appearing around the 26th day of the 34- to 35-day incubation period (Hochel et al., 1999). Similar findings of differential developmental onset of sympathetic and parasympathetic cardiovascular regulation have also been reported in fishes, amphibians, and other species of birds (for reviews see Burggren and Pinder, 1991; Burggren and Just, 1992; Burggren and Crossley, 2002; also Fritsche and Burggren, 1996; Jacobsson and Fritsche, 1999; Fritsche et al., 2000; Crossley et al., 2003; Kloberg and Fritsche, 2002).

Whether the regulatory systems of other organs systems show asynchronous sympathetic and parasympathetic development remains uncertain, only underscoring the importance of not assuming that embryonic systems are dually innervated when they first begin to function in the embryo.

6. Assumption: phylogeny dictates physiology in embryos as in adults

Most biologists are highly wary of phrases such as "the vertebrate heart", "the invertebrate nervous system", or even the "mammalian stomach": there are at least a half dozen fundamentally different vertebrate heart plans, dozens of different invertebrate neural layouts, and major differences in gut structure in mammalian ungulates and

carnivores. Sensitive to this taxonomic diversity, physiologists tend to view animals different from those we are directly interested in as either "models" at best, or even as irrelevant to our own lines of study.

While comparable data are in short supply, cross-species comparisons of physiological values and rates from even quite taxonomically diverse species indicate surprisingly common physiological similarities early in development. Nowhere is this more evident than in the developing circulation. While the circulation of fishes, amphibians, bids and reptiles is categorized by major differences in arterial pressures and in the "plumbing" of the various vascular beds, there are unexpected similarities in physiological performance during early development. These similarities are not only qualitative, but even quantitative. For example, consider a comparison of blood pressure early in the development of a wide range of vertebrates (Fig. 3). Irrespective of whether measurements are from the avian heart, which will subdivide and form a high pressure systemic and low pressure pulmonary circulation at birth, or from the relatively low-pressured single ventricle of the fish, the initial blood pressures in comparably early stages of vertebrate taxa are quite comparable, even in diverse taxa with very different sized embryos. Even when absolute blood pressures differ, the *pattern* of blood pressure increase during development shows broad similarity.

How does this observation of a relatively similar early developmental pattern of cardiovascular performance help developmental physiologists? As long as one focuses on the early developmental period, the term "vertebrate heart"
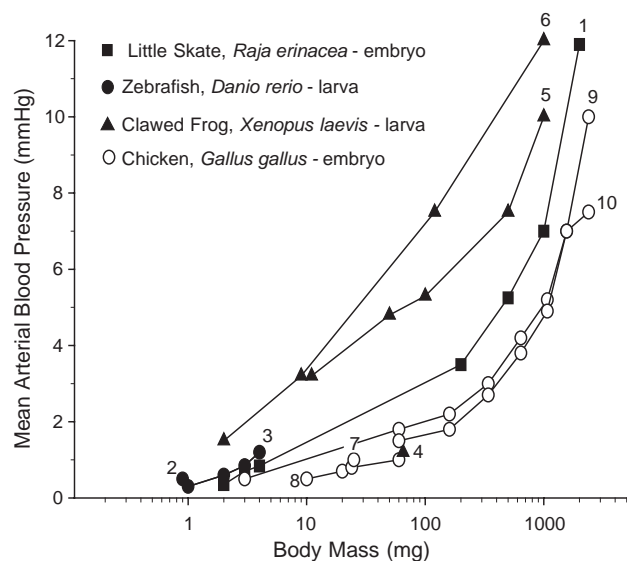

Fig. 3. Changes in mean arterial blood pressure as a function of body mass increase during development in fish, amphibian and bird larvae and embryos. References: (1) Pelster and Bemis, 1992; (2) Pelster and Burggren, 1996; (3) Hu et al., 2000; (4) Warburton and Fritsche, 2000; (5) Hou and Burggren, 1995; (6) Fritsche and Burggren, 1996; (7) Nakazawa and Kajio, 1997; (8) Keller, 1997; (9) van Mierop and Bertuch, 1967; (10) Girard, 1973.

takes on new validity. Thus, if initially generated blood pressures (and perhaps wall stress, force generation, etc.) are so similar despite the major anatomical differences that are soon to unfold, then perhaps there are some general principles that guide the function of hearts as they assemble. If this holds, then developmental physiologists can be even more opportunistic, ranging farther from a few typical animal models. Instead of investigating the "usual suspects", developmental physiologists may decide to exploit the early embryos and larvae of less studied animals whose early developmental stages lend themselves to easier investigation because they are larger, more transparent, or have other characteristics that advocate their further exploration (see Burggren, 2000).

7. Summary

Interest in comparative developmental physiology is burgeoning (Warburton et al., in press), as are the assumptions we import from studies of the physiology of mature animals. Assumptions, be they in developmental physiology, macroeconomics or musicology, are essential to move any field forward. More specifically, assumptions are an important part of any discipline's models. Indeed, at one level, assumptions are simple models, in which we organize the combination of what we know and what we think we know into one convenient package that guides our future actions. Yet, when we fail to test our most comfortable assumptions on a regular basis, they quickly pass into dogma and, if left unchallenged, into "truth".

As evident from this essay, as ecological physiologists anxious to build this field, we have overly-eagerly imported into developmental physiology a series of key assumptions regarding the influence on physiology of allometry, complexity, functionality and phylogeny. While these assumptions have well served the study of adult animals (and, indeed, are regularly tested and affirmed for adults), they may be problematic when directly applied to developing animals. Thus, one of the greatest challenges to developmental physiologists is to ensure that we modify our pet assumptions, which in many cases will mean increasing the sophistication of the assumption to mirror our increasingly sophisticated knowledge of the physiology of developing animals.

This essay has challenged only a few of many key assumptions that we use in developmental physiological studies. Any value to its message may be less about these particular examples than about a confronting our physiological assumptions wherever we find them in our experiments on developing animals. Finally, irony is abundant in the fact that by assailing old dogmas we contribute to the creation of new ones. Perhaps Bertrand Russell (1892–1970) offered the most appropriate caution: "What the world needs is not dogma but an attitude of scientific inquiry..."

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