

The Mathematics of Growth

Developmental biology has been described as the last refuge of the mathematically incompetent scientist. This phenomenon, however, is not going to last. While most embryologists have been content trying to analyze specific instances of development or even formulating some general principles of embryology, some researchers are now seeking the *laws* of development. The goal of these investigators is to base embryology on formal mathematical or physical principles (see Held 1992; Webster and Goodwin 1996). Pattern formation and growth are two areas in which such mathematical modeling has given biologists interesting insights into some underlying laws of animal development.

The mathematics of organismal growth

Most animals grow by increasing their volume while retaining their proportions. Theoretically, an animal that increases its weight (volume) twofold will increase its length only 1.26 times (as $1.26^3 = 2$). W. K. Brooks (1886) observed that this ratio was frequently seen in nature, and he noted that the deep-sea arthropods collected by the *Challenger* expedition increased about 1.25 times between molts. In 1904, Przibram and his colleagues performed a detailed study of mantises and found that the increase of size between molts was almost exactly 1.26 (see Przibram 1931). Even the hexagonal facets of the arthropod eye (which grow by cell expansion, not by cell division) increased by that ratio.

D'Arcy Thompson (1942) similarly showed that the spiral growth of shells (and fingernails) can be expressed mathematically ($r = a^\theta$), and that the ratio of the widths between two whorls of a shell can be calculated by the formula $r = e^{2\pi \cot \theta}$ (Figure 1). Thus, if a whorl were 1 inch in breadth at one point on a radius and the angle of the spiral were 80° , the next whorl would have a width of 3 inches on the same radius. Most gastropod (snail) and nautiloid mollusks have an angle of curvature between 80° and 85° .* Lower-angle curvatures are seen in some shells (mostly bivalves) and are common in teeth and claws.

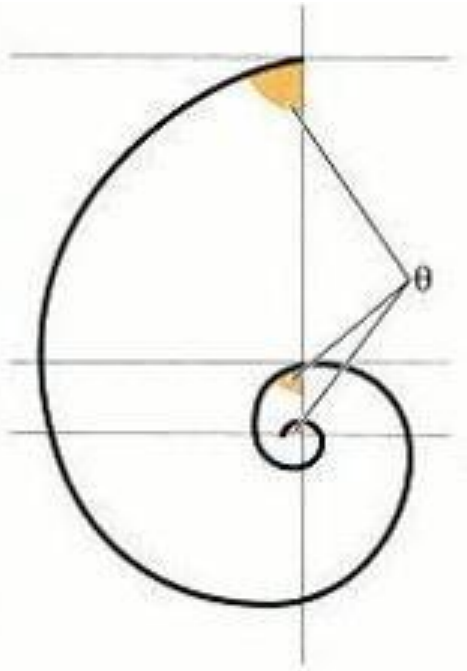


Figure 1 Equiangular spiral growth patterns. René Descartes' analysis of an equiangular spiral, showing that if the curve cuts each radius vector at a constant angle (symbolized by theta;), then the curve grows continuously without ever changing its shape. (After Thompson 1942.)

Such growth, in which the shape is preserved because all components grow at the same rate, is called isometric growth. In many organisms, growth is not a uniform phenomenon. It is obvious that there are some periods in an organism's life during which growth is more rapid than in others. Physical growth during the first 10 years of person's existence is much more dramatic than in the 10 years following one's graduation from college. Moreover, not all parts of the body grow at the same rate. This phenomenon of the different growth rates of parts within the same organism is called allometric growth (or allometry). In humans, arms and legs grow at a faster rate than the torso and head, such that adult proportions differ markedly from those of infants. Julian Huxley (1932) likened allometry to putting money in the bank at two different continuous interest rates.

The formula for allometric growth (or for comparing moneys invested at two different interest rates) is $y = bx^{a/c}$, where a and c are the growth rates of two body parts, and b is the value of y when $x = 1$. If $a/c > 1$, then that part of the body represented by a is growing faster than that part of the body represented by c . In logarithmic terms (which are much easier to graph), $\log y = \log b + (a/c)\log x$.

One of the most vivid examples of allometric growth is seen in the male fiddler crab, *Uca pugnax*. In small males, the two claws are of equal weight, each constituting about 8% of the crab's total weight. As the crab grows larger, its chela (the large crushing claw) grows even more rapidly, eventually constituting about 38% of the crab's weight (Figure 2). When these data are plotted on double logarithmic plots (the body mass on the x axis, the chela mass on the y axis), one obtains a straight line whose slope is the a/c ratio. In the male *Uca pugnax* (whose name is derived from the huge claw), the a/c ratio is 6:1. This means that the mass of the chela increases six times faster than the mass of the rest of the body. In females of the species, the claw remains about 8% of the body weight throughout growth. It is only in the males (who use the claw for defense and display) that this allometry occurs.



Figure 2 In this male fiddler crab, Allometric growth occurs only in one of the male's claws. In females (not shown), both claws retain isometric growth. (Rushen! on VisualHunt / CC BY-SA.)

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