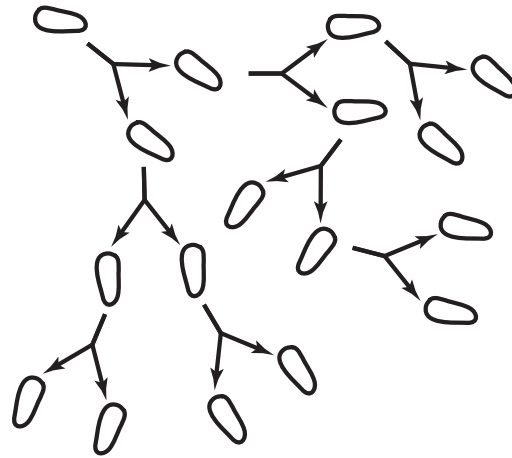


Biological organisms normally exhibit some type of life cycle –growth, development and reproduction– which has evolved to enhance survivability and adaptability. Survival implies successful reproduction to continue the species; adaptability implies the ability of the organisms to adapt to environmental (and other) challenges during its reproductive lifetime.

One of the simplest life cycles is that of a prokaryote. Prokaryotes usually divide by binary fission:

The lifecycle, from one to two to four cells, etc., is usually described by the generation time (the doubling time –the time required for a cell division to occur). The doubling time depends on nutrient supply, temperature and other conditions. Under optimal conditions, doubling is about 20–80 minutes. In the absence of any constraints on continued growth –*ad infinitum*– population growth will follow the relation:

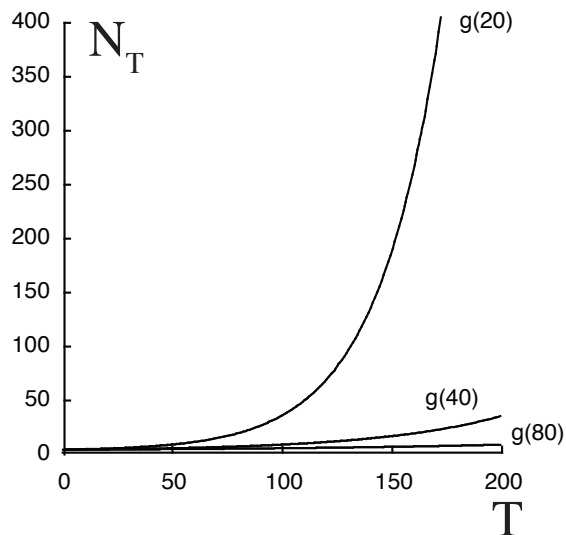


$$N_T = N_0 \cdot 2^{(T/g)}$$

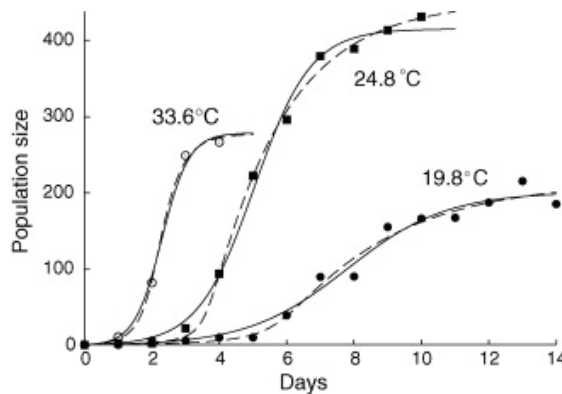
g is the generation time
 N_0 is the number of cells at time $T = 0$
 N_T is the number of cells at time T

as time increases, $t/g = 1, 2, 3 \dots$, thus $2^1, 2^2, 2^3$, etc.

Implicit in the process of binary fission is the concept that DNA will be duplicated and passed on from the ‘mother’ cell to the two ‘daughter’ cells. Mutations can occur during DNA replication. Mutations will increase genomic variability through the many bacterial generations. The age of the bacteria is remarkable: The progenitor of any bacteria existing now appeared 3 to 4 billion years ago.



It is important to emphasize the complexity of growth. The simple exponential growth process can and does occur under some conditions, but constraints on growth are many. Growth of the individual may or may not be determinant (stopping at a well-defined endpoint, a good example is human (animal) development). Growth of a population will decline as resources are exhausted (humanity may become a good example ...). Below is just one example of population growth over time:



These are population growth curves for the organism *Moina macrocopa*. The data are from Terao, A. and T. Tanaka (1928) Population growth of the water-flea, *Moina macrocopa* Strauss. Proc. Imper. Acad. Jpn. Vol. 4, pp. 550–552. It's an example of how temperature affects the doubling time (fastest at 33.5 degrees) and the population size (maximal at 24.8 degrees^[1]).

The data can be fit by a logistic growth curve:
$$N_T = \frac{K \cdot N_0 \cdot e^{T/g}}{K + N_0(e^{T/g} - 1)}$$
 K is the carrying capacity

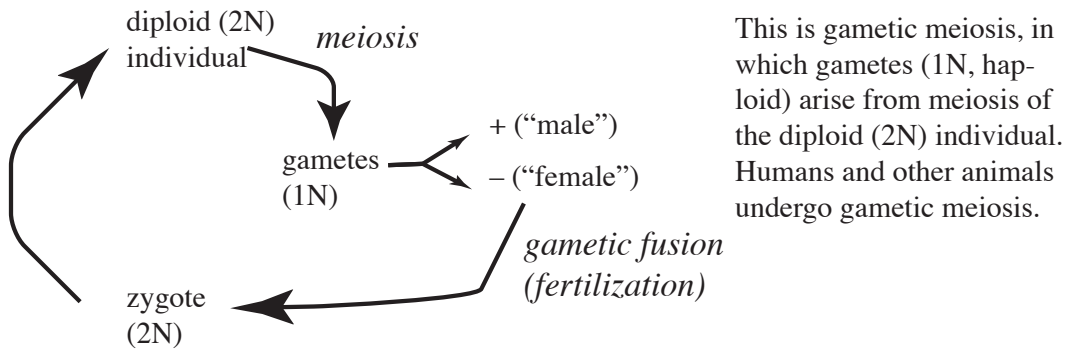


Moina macrocopa is a Crustacean, commonly growing in fresh waters. It is capable of undergoing parthenogenesis: Assexual reproduction. That is, the egg does not require fertilization by a male to develop into an embryo. Parthenogenesis is seen most commonly in plants and in some invertebrates, and rarely in vertebrates (Komodo dragon offspring may arise through parthenogenesis).

An example of chaotic growth is described on page 1.13.

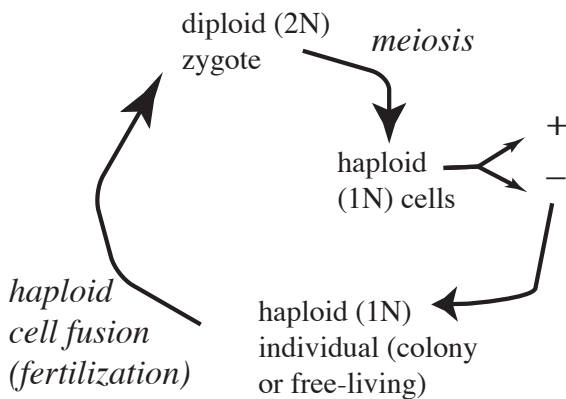
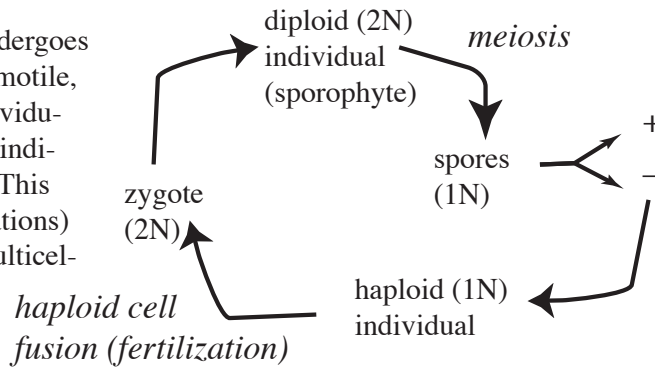
[1] Data were redrawn by Seiichi Sakanoue in a recent publication: Sakanoue, S. (2007) Extended logistic model for growth of single-species populations. Ecological Modelling 205(1-2):159-168. The article describes the multitude of equations which are used to predict not only the sigmoidal characteristic of growth of organisms and populations, but also many economic processes. The complexity of the mathematical models can be daunting, especially when the multi-variate nature of carrying capacity must be considered. Even more complex is the challenge of incorporating predator-prey relations. The Lotka-Volterra model describing predator-prey effects on predator (x) - prey (y) populations is a pair of coupled non-linear differential equations: $dx/dt = x(\alpha - \beta y)$ and $dy/dt = y(\gamma - \delta x)$.

Not only is growth complex, but eukaryotic life cycles typically involve coordinated exchange of genetic material between individuals. Even prokaryotes are capable of exchanging DNA, either via plasmids or in a process called conjugation. Amongst the eukaryote clades, there are a variety of mechanisms for exchanging DNA: All involve the alternation between haploid and diploid states in Sexual Cycles that are defined by how and when in the life cycle DNA is shared: Gametic, Sporic and Zygotic.



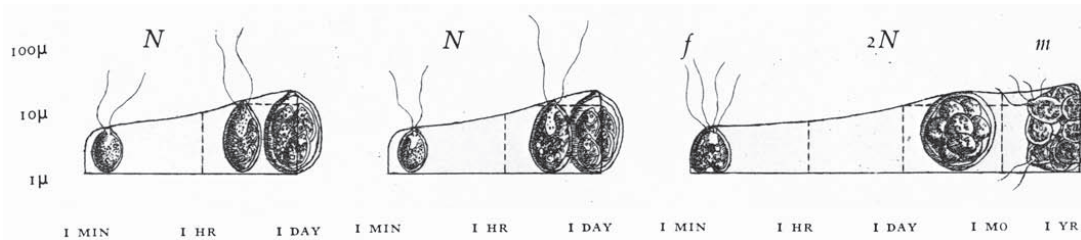
This is gametic meiosis, in which gametes (1N, haploid) arise from meiosis of the diploid (2N) individual. Humans and other animals undergo gametic meiosis.

In sporic meiosis, the diploid undergoes meiosis to produce spores (non-motile, which develop into haploid individuals. Cells of the + and - haploid individuals fuse to form the zygote. This life cycle (Alternation of Generations) is common among plants and multicellular algae.



Zygotic meiosis is common in unicellular protists and yeasts (and other members of the Fungal Kingdom).

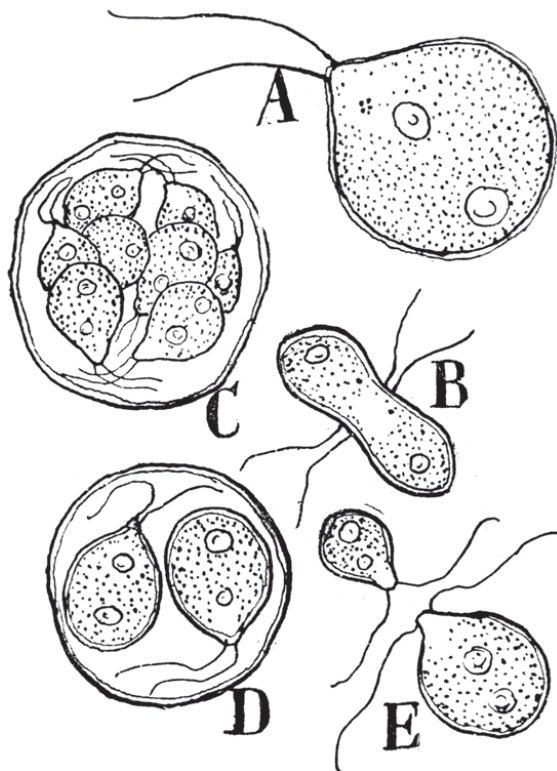
Some examples of biological life cycles are shown in this and the following pages. The source is John Tyler Bonner's book "Size and Cycle. An Essay on the Structure of Biology" published in 1965 by the Princeton University Press. Note that the y-axis (length) and x-axis (time) are both log scales.



Chlamydomonas Reinhardtii

The first two cycles show the asexual reproduction of the haploid individual. The last cycle shows the sexual cycle with fertilization, encystment of the zygote, and meiosis, which is followed by liberation of the new haploid individuals.

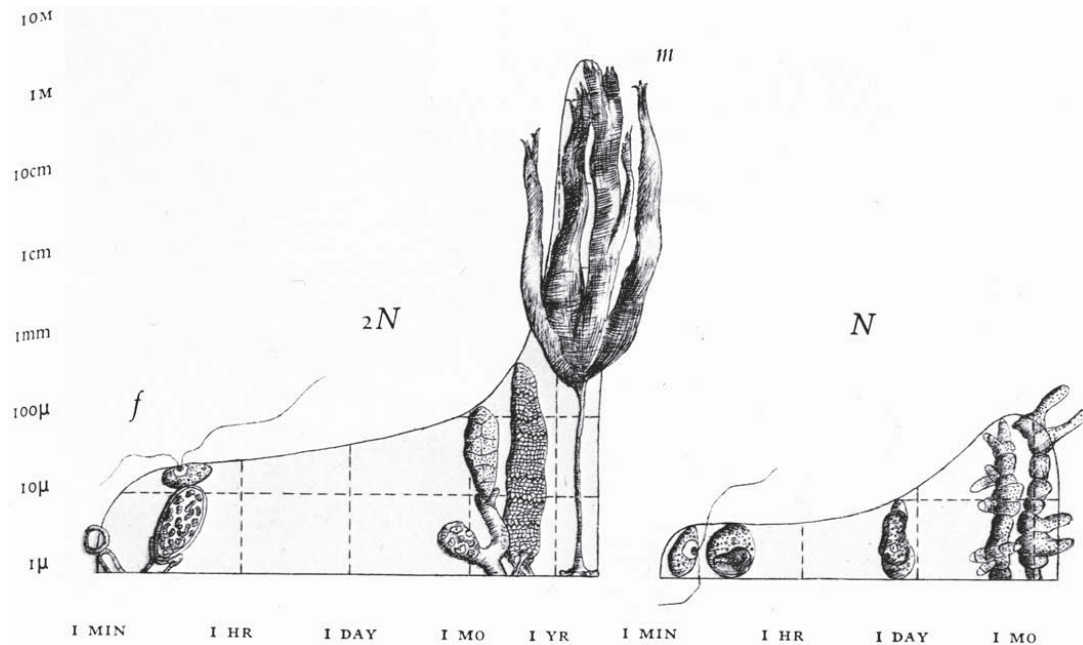
Nota bene: The generation time is about 6–7 hours for unicellular protists. Their size is normally in the range of 20–40 microns.



Chlamydomonas Reinhardtii is an example of a unicellular protist, growing in freshwater. It can grow either heterotrophically or autotrophically. It is a model organism for genetic studies.

The illustration shows the features in the life history of *Chlamydomonas*: A, character of the motile alga. B, conjugation of isogamous gametes. C, an alga dividing to form numerous small male gametes. D, a cell forming two large female gametes. E, male and female gametes about to conjugate.

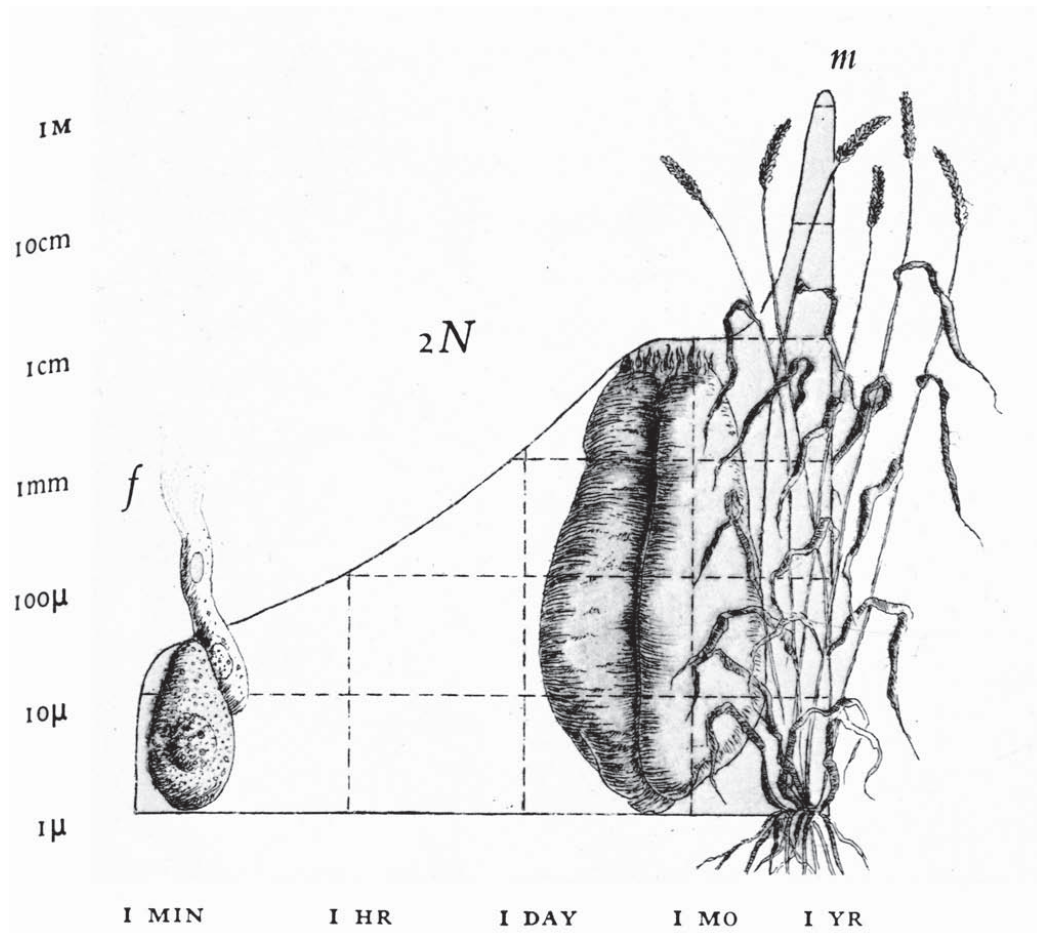
Source: Carlton C. Curtis, *Nature and Development of Plants* (New York: Henry Holt Company)



Laminaria flexicaulis

This large brown alga or kelp is a multicellular algae which has an alternation of generations. The haploid generation is small and inconspicuous (second cycle) especially in comparison with the huge diploid generation (first cycle). In the big frond, there is a distinct growth zone at the junction of the blades and the stipe, and considerable cell differentiation, especially in the stipe, where there are cells specialized for conduction.

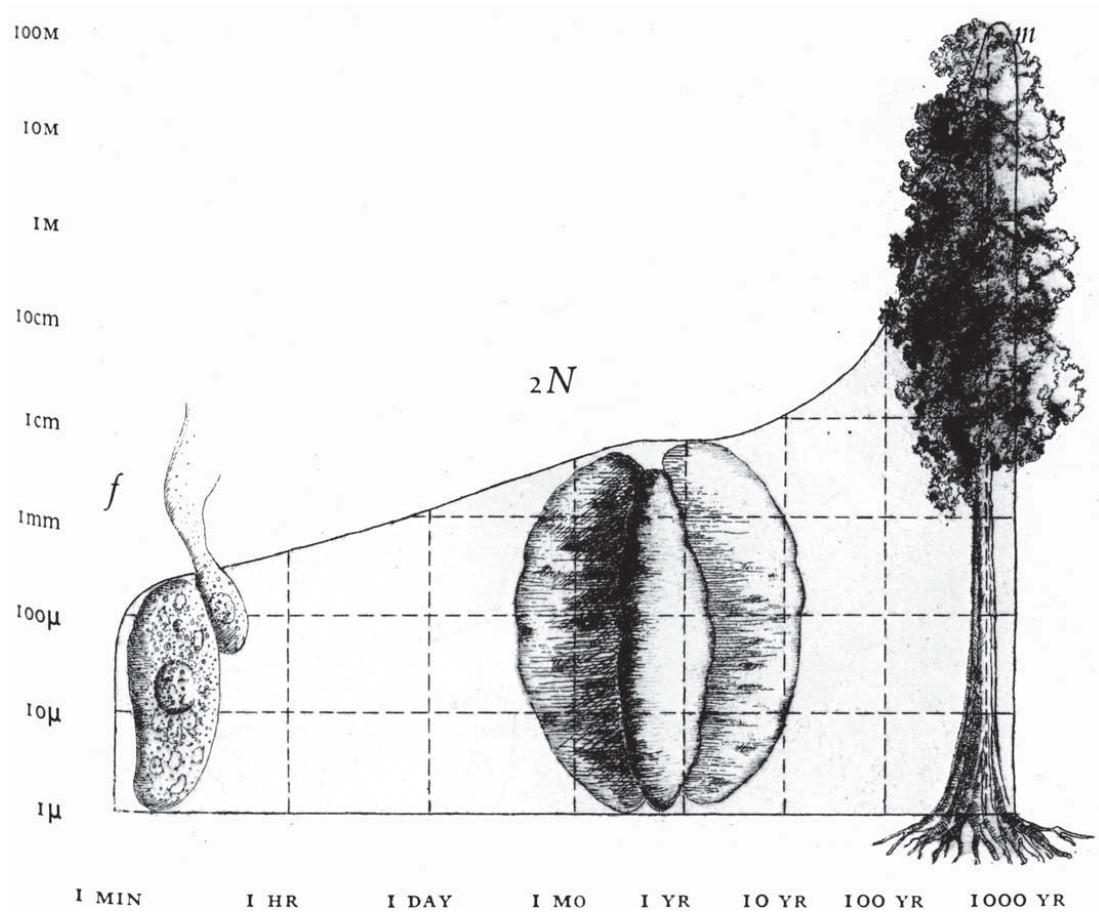
Nota bene: A multicellular photosynthetic organism (one of the brown algae, Phaeophyta), *Laminaria* is very large (often 20 meters in length) with a generation time in the range of 2 years.



Triticum aestivum

Wheat, like all higher plants, is characterized by having seeds. This is a dormant stopping place which interrupts the period of size increase. There is growth between fertilization and seed formation, a period of equilibrium, and subsequent growth upon seed germination. Wheat is an annual plant and therefore there is no cambium or secondary thickening. After a single spurt of growth in one season, the main body of the plant turns yellow and dies.

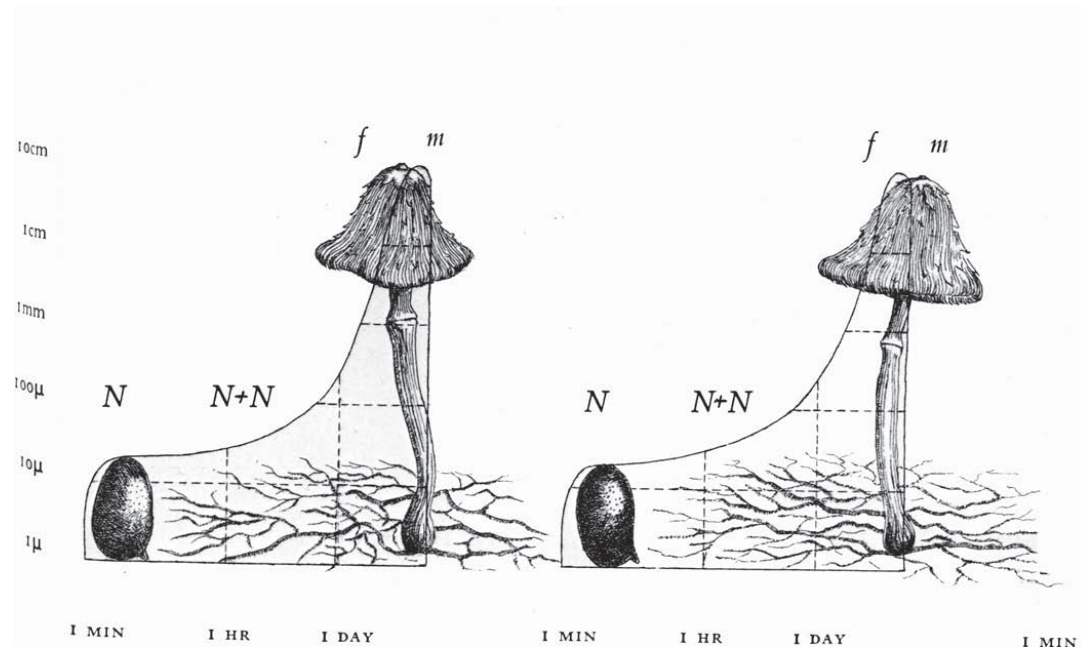
Nota bene: Wheat is an example of a land-dwelling multicellular photosynthetic organism with a proscribed life cycle of one year (hence, an “annual plant”), tuned to the changing seasons of a **Life Cycles** temperate climate. Other land plants (perennials) have adapted to survival through the seasons, or grow in tropical regions without well-defined seasons.



Sequoia gigantea

Sequoia is the largest of the trees. Fertilization and the early growth of the seed are essentially the same as annual plants, such as wheat. Because of the cambium and secondary thickening, the size of the tree can increase enormously. Sequoia does not begin to set seed until it is 60 years old and 80 meters high.

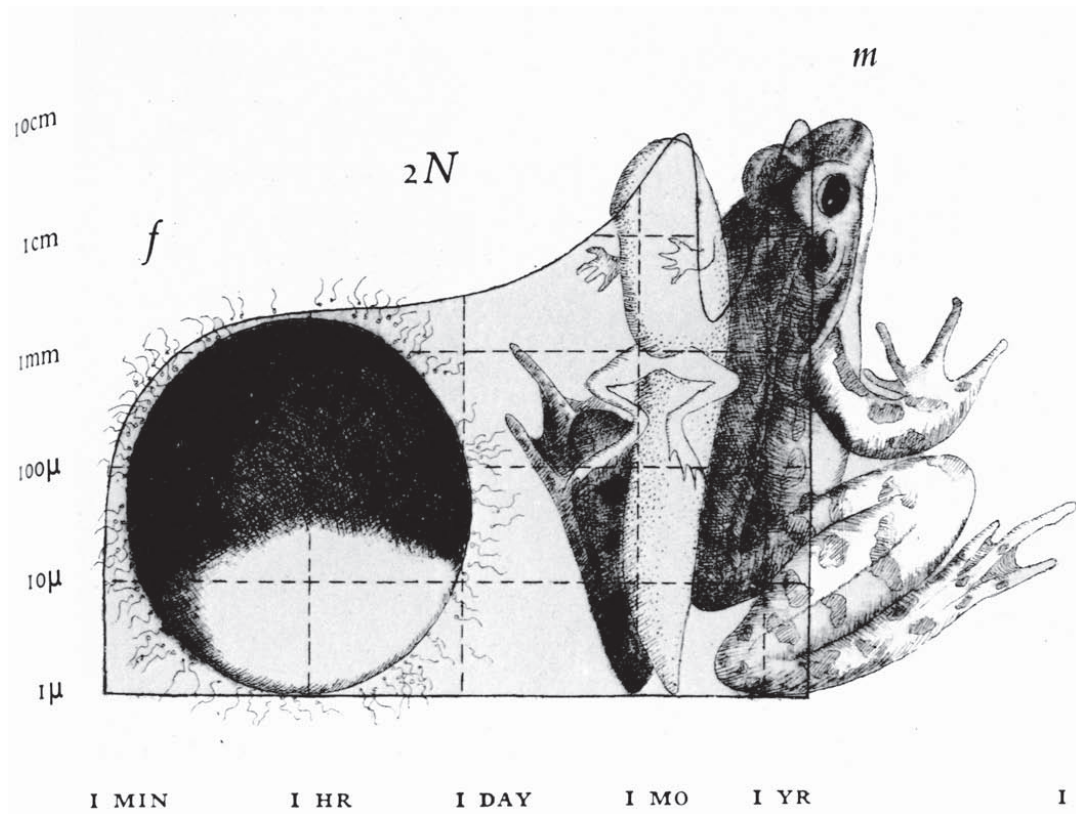
Nota bene: The Sequoia is an example of an extreme within the Plant Kingdom: large size and long lifetime (attaining an age of 1000 years or so, and having a generation time of 60 years).



Coprinus sterquilinus

In mushrooms the hypha that emerges from the germinating spore is haploid and gives rise to the primary mycelium. Primary mycelia of compatible mating types will fuse and the nuclei of both will come together in pairs and remain in close association. This is the dikaryon condition found in the secondary mycelium and indicated as $N + N$ in the illustration. Final nuclear fusion or karyogamy only occurs in the subterranean mycelium, and the protoplasm from this mycelium flows into the fruiting body in a matter of hours.

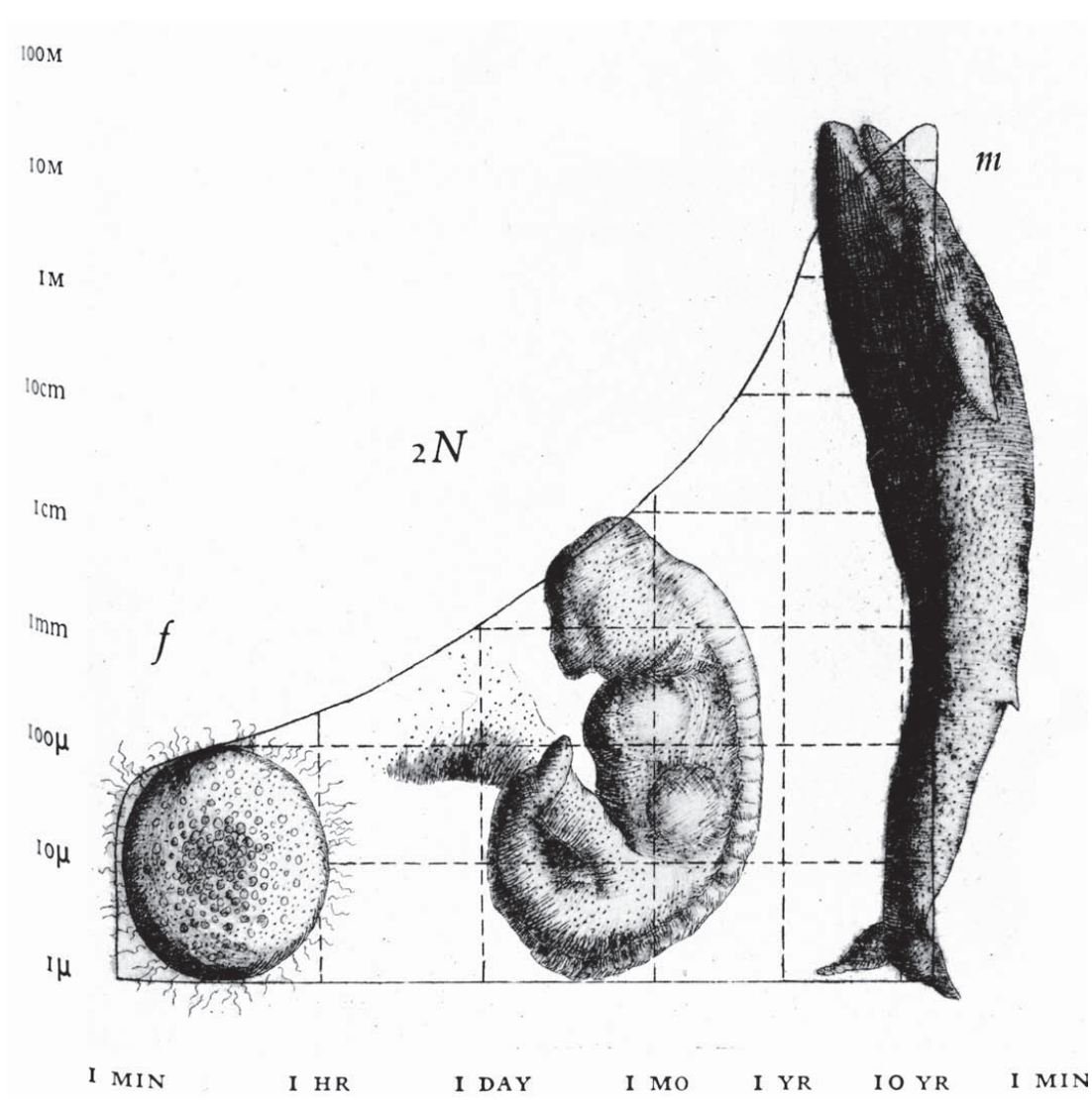
Nota bene: The Fungal Kingdom represents a large clade of organisms, analogous to the Prokaryotic, Protist, Plant and Animal Kingdoms. Fungi are most closely related to the Animal Kingdom. Organismal size can vary from the microscopic to individuals of enormous mass, though 'hidden' within the soil. Generation times are correspondingly diverse: Unicellular yeasts may have generation times almost as fast as bacteria (60 minutes or so). Other species may grow solely vegetatively, and only complete a sexual generation when they encounter a member of the same species, but of the opposite mating type.



Rana pipens

Metamorphosis in the frog involves the loss of the tail and therefore a minor size reduction.

Nota bene: An example from the Animal Kingdom. The frog has a length in the range of 6.0 cm, and a generation time of about 1.5 years.

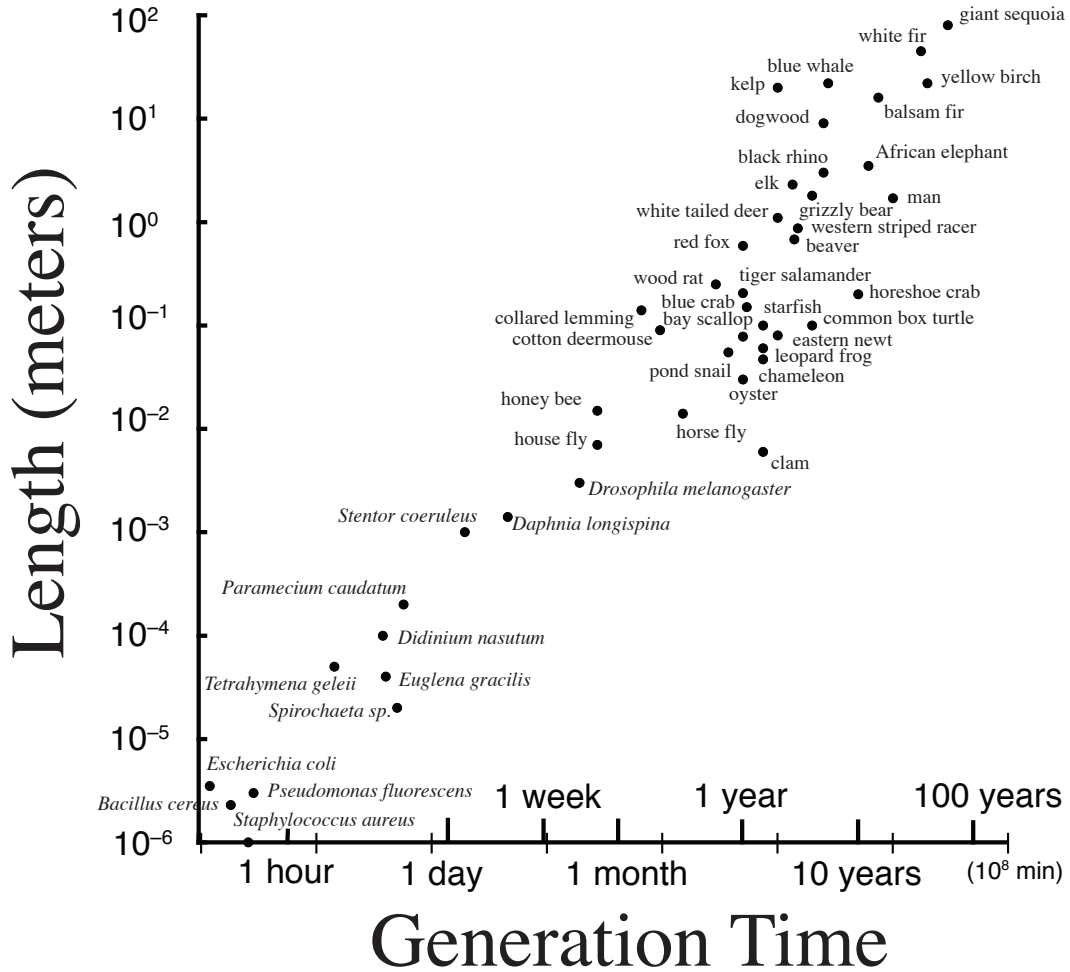


Balaenoptera musculus

The blue whale is the largest animal.

Nota bene: The whale is first capable of reproduction when it is 6 years of age and 22 meters long.

Here is a compilation of size *versus* generation time from John Tyler Bonner’s book “Size and Cycle. An Essay on the Structure of Biology published in 1965 by the Princeton University Press. Note that the y-axis (length) and x-axis (time) are both log scales. The examples come from all the kingdoms (except the Fungal Kingdom, which, as noted, usually lacks a defined generation time).



Nota bene: Of greatest interest to Bonner, and to others, is the relation between size and generation time. This is best observed when sampling from a full range of biological organisms, from bacteria and protists to trees and whales. To some extent, increased size and generation time occurred later in evolutionary time, but in fact, this may have more to do with the development of multicellular biological architecture, an event which occurred only 1,500 million years ago, or so. Speculations on the necessity of a cycle of sexual reproduction (what advantages does it really confer?) and the reasons for the striking correlation between size and generation time, are frankly, in the realm of a Philosophy of Biology, since we are unable to perform experiments of the magnitude and epochal time required to construct experimental tests for any given hypothesis.

Species	Length	generation time	reference
Staphylococcus aureus	1 μm	27 min	μ
Bacillus cereus	2.3 μm	19 min	μ
Pseudomonas fluorescens	3 μm	30 min	μ
Escherichia coli	3.5 μm	12.5 min	μ
Spirochaeta sp.	20 μm	8.8 hours	μ
Euglena gracilis	40 μm	7 hours	μ
Tetrahymena geleii	50 μm	2.5 hours	μ
Didinium nasutum	100 μm	6.6 hours	μ
Paramecium caudatum	200 μm	10 hours	μ
Stentor coeruleus	1 mm	34 hours	G
Daphnia longispina	1.4 mm	80 hours	BH
Drosophila melanogaster	3 mm	14 days	
Venus mercenaria (clam)	6 mm	1.5 years	BH
Musca domestica (house fly)	7 mm	20 days	BH
Tabanus atratus (horse fly)	14 mm	110 days	BH
Apis mellifera (honey bee)	15 mm	20 days	BH
Crassostrea virginica (oyster)	30 mm	1 year	BH
Anolis carolinensis (chameleon)	47 mm	1.5 years	BH
Lymnaea stagnalis (pond snail)	55 mm	9 month	BH
Rana pipiens (leopard frog)	60 mm	1.5 years	BH
Aequipecten irradians (bay scallop)	78 mm	1 year	BH
Diemictylus viridescens (eastern newt)	80 mm	2 years	BH
Peromyscus gossypinus (cotton deer mouse)	90 mm	70 days	M
Asterias forbesi (starfish)	100 mm	1.5 years	BH
Terrapene carolina (common box turtle)	100 mm	4 years	BH+G
Dicrostonyx groenlandicus (collared lemming)	140 mm	48 days	BH
Callinectes sapidus (blue crab)	150 mm	13 months	BH
Limulus polyhenus (horseshoe crab)	200 mm	10 years	BH
Ambystoma tigrinum (tiger salamander)	205 mm	1 year	BH
Neotoma floridana (wood rat)	250 mm	7 months	BH
Vulpes fulva (red fox)	590 mm	1 year	BH
Castor canadensis (beaver)	680 mm	2.8 years	BH
Masticophis taeniatus (western striped racer)	870 mm	3 years	BH
Odocoileus virginianus (white tailed deer)	1.1 M	2 years	BH+G
Homo sapiens (man)	1.7 M	20 years	G
Ursus horribilis (grizzly bear)	1.8 M	4 years	BH+M
Cervus canadensis (elk)	2.3 M	2.7 years	BH+M
Diceros bicornis (black rhino)	3.0 M	5 years	G
Loxodonta africana (African elephant)	3.5 M	12.3 years	BH
Cornus florida (dogwood)	9.0 M	5 years	G
Abies balsamea (balsam fir)	16 M	15 years	G
Nerocystis Luetkeana (kelp)	20 M	2 years	F
Betula alleghaniensis (yellow birch)	22 M	40 years	G
Balaenoptera musculus (blue whale)	22 M	5.5 years	BH+M+S
Abies concolor (white fir)	45 M	35 years	G
Sequoia gigantea (giant sequoia)	80 M	60 years	G

BH: Handbook of Biological Data, ed. By WS Spencer

G: Biological Handbook: Growth, ed by PL Altman and DS Dittmer

M: The Mammal Guide, by RS Palmer

S: Whales, by EJ Slipper

F: Frye, Bot Gaz (1906)

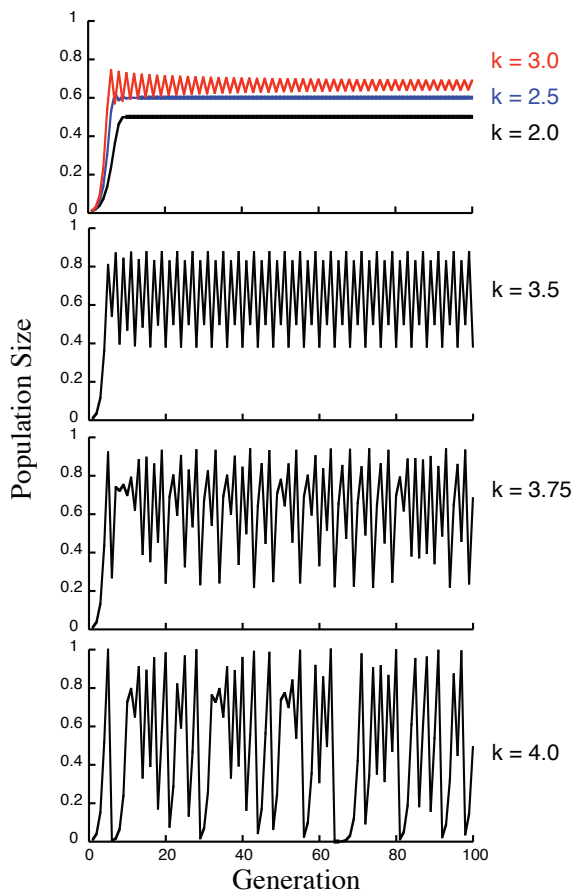
Data presented in Bonner JT 1965 Size and Cycle.

An essay on the structure of biology
Princeton Univ Press. pages 16 and 17

The relations between biophysical modeling of growth and real biological populations are often tenuous, so that models must be used with extreme caution. Even so, models can reveal the unexpected. The equation below is a typical logistic growth equation, in which the past population (X_t) affects the current population (X_{t+1}) (because of the term $1-X_t$), where t is the generation.

$$X_{t+1} = kX_t(1 - X_t)$$

k is the unrestrained capacity for population increase. As it changes, so do the population dynamics, as shown in the graphs^[1].



At relatively low capacity for unconstrained growth (k -values of 2.0 and 2.5), the population increases to a steady state level, where population growth is stably constrained by the population itself. But as the capacity for unconstrained growth increases (k -values of 3.0 and 3.5), there is a well-defined periodic change in population size: Still stable, but fluctuating around some mean value. If the growth capacity is increased beyond this point (k -values of 3.75 to 4.0), the population size begins to change chaotically over generations, a pattern of high populations followed by catastrophic crashes to near zero.

It is a fascinating idea: that chaos is embedded in such a 'simple' logistic growth equation. And, sometimes, real biological populations do fluctuate chaotically, although the underlying causes are certainly far more complex than such a simple equation would suggest.

[1] Source: Stewart, Ian Seventeen (2012) In Pursuit of the Unknown: 17 equations that changed the world. Basic Books. Chapter 16.