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Basic concepts

The purpose of this chapter is to introduce some general concepts to prepare for the development of the simplest version of DEB theory, which is discussed in the next chapter. I start with the explanation why the organisation level of the individual plays a key role in DEB theory, followed by homeostasis concepts. Mechanisms for homeostasis and evolutionary aspects are discussed later. Then we need to introduce the notion of life stages and effects of temperature in some detail.

1.1 Individuals as dynamic systems

1.1.1 The basic level of metabolic organisation

From a systems analysis point of view, individuals are special for metabolic organisation because at this organisational level it is relatively easy to make energy and mass balance. This is important, because the conservation law for energy and mass is one of the few hard laws available in biology. At the sub- and supra-individual levels it is much more difficult to measure and model mass and energy flows.

Life started as an individual in evolutionary history, see {386}, and individuals are the units of selection and the survival machines of life; differences between individuals are, in combination with selection, key to evolution. DEB theory captures these differences by parameter values, which can differ between individuals, see Chapter 8.

Individuals are also special because behaviour is key to food intake and food selection (food fuels metabolism) and to mate selection; reproduction controls survival across generations in many species.

The analysis of metabolic organisation should, therefore, start at the level of the individual. Many species are unicellular, which links subcellular organisation directly to the individual level.

1.1.2 Vague boundaries: the cell–population continuum

The emphasis on individuals should not mask that the boundaries between cells, individuals, colonies, societies and populations are not always sharp. Fungal mycelia can

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cover up to 15 hectares as in the basidiomycete *Armillaria bulbosa*, but they can also fragment easily. Cellular slime moulds (dictyostelids) have a single-celled free-living amoeboid stage, as well as a multicellular one; the cell boundaries dissolve in the multicellular stage of acellular slime moulds (Eumycetozoa), which can now creep as a multi-nucleated plasmodium over the soil surface.

The mycetozoans are not the only amoebas with multi-nuclear stages; *Mastigamoeba* (a pelobiont) is another example [88]. Many other taxa also evolved multi-nucleated cells, plasmodia or stages, e.g. ciliates, xenophyophores, actinophryids, *Biomyxa*, loukozoans, diplomonads, Gymnosphaerida, haplosporids, Microsporidia, nephridiophagids, Nucleariidae, plasmodiophorids, Pseudospora, Xanthophyta (e.g. *Vaucheria*), most classes of Chlorophyta (Chlorophyceae, Ulvophyceae, Charophyceae (in mature cells) and all Cladophoryceae, Bryopsidophyceae and Dasycladophyceae) [516, 871]. Many higher fungi have hyphen where cells are fused in a multi-nucleated plasma, and nuclei of several rhodophytes can crawl from one cell into another. The Paramyxea have cells inside cells. The Myxozoa have multicellular spores, but a single-cellular adult stage. Some bacteria have multicellular tendencies [1044].

Certain plants, such as grasses and sedges, can form runners that give off many sprouts and cover substantial surface areas; sometimes, these runners remain functional in transporting and storing resources as tubers, whereas in other cases they soon disintegrate. A similar situation can be found in, for example, corals and bryozoans, where the tiny polyps can exchange resources through stolons.

Behavioural differentiation between individuals, such as between those in syphonophorans, invites to consider the whole colony an integrated individual, whereas the differentiation in colonial insects and mammals is still so loose that it is recognised as a group of coordinated individuals. Schools of fish {348}, bacterial colonies and forests {134} can behave as a super-individual,

These examples illustrate the vague boundaries of multicellularity, and even those of individuality. A sharpening of definitions or concepts may reduce the number of transition cases to some extent, but this cannot hide the fact that we are dealing here with a continuum of metabolic integration in the twilight zone between individuals and populations. This illustrates that organisms, and especially eukaryotes, need each other metabolically.

1.1.3 Why reserves apart from structure?

DEB theory partitions biomass into one or more reserves and one or more structures. Reserves complicate the dynamics of the individual and the application of the model considerably, so it makes sense to think about its necessity and become motivated to deal with this more complex dynamics.

We need reserve for the following reasons:

- to include metabolic memory. A variable substrate (food) supply does not combine easily with constant maintenance needs. Organisms use reserve(s) to smooth out fluctuations. The metabolic behaviour of an individual does not depend on the actual food availability, but of that of the (recent) past. Individuals react slowly to changes in their feeding conditions. This cannot be described realistically with the digestive system as a buffer, because its relaxation time is too short. Spectacular examples of prolonged action without food intake are the European, North American and New Zealand eels, *Anguilla*, which stop feeding at a certain moment. Their alimentary canal even degenerates, before the 3000-km-long journey to their breeding grounds where they spawn. The male emperor penguin *Aptenodytes forsteri* breeds its egg in Antarctic midwinter for 2 months and feeds the newly hatched chick with milky secretions from the stomach without access to food. The male loses some 40% of its body weight before assistance from the female arrives.

- to smooth out fluctuations in resource availability to make sure that no essential type of resource is temporarily absent {394}; growth can only proceed if all essential resources are available in certain relative amounts. This argument concerns a different form of memory that is used by multiple reserve systems. Single reserve systems evolved from multiple reserve systems. This will be discussed in Chapter 10. Non-limiting reserves can dam up, which causes strong changes in the composition of biomass, see {197}.
- the chemical composition of the individual depends on the growth rate. This can only be captured if biomass has more than one component.
- fluxes (e.g. dioxygen, carbon dioxide, nitrogen waste, heat) are linear sums of three basic energy fluxes: assimilation, dissipation and growth (as we will see). The method of indirect calorimetry is based on this fact. Without reserve, using a single structure only, two rather than three basic energy fluxes would suffice, while experimental evidence shows that this is not true.
- to explain observed patterns in respiration and in body size scaling relationships. Eggs decrease in mass during development, but increase in respiration, while juveniles increase in mass as well as in respiration. This cannot be understood without reserve. A freshly laid egg consists (almost) fully of reserve and hardly respires; a simple and direct empirical support for the DEB assumption that structure requires maintenance, but reserve does not. We will see that reserve plays a key role in body size scaling relationships, and to understand, for instance, why respiration increases approximately with weight to the power 3/4 among species.
- to understand how the cell decides on the use of a particular (organic) substrate, as building block or as source of energy. This problem will be discussed in the section on organelle–cytoplasm interactions at {282}.

The term reserve does *not* mean 'set apart for later use'; reserve 'molecules' can have active metabolic functions while 'waiting' for being used. Ribosomal RNA, for instance, turns out to belong to the reserve, see {143}; it is used for peptide elongation. The primary difference between reserve and structure is in their dynamics:

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all chemical compounds in the reserve have the same turnover time, in the structure they can be different. Reserves are used to fuel all metabolic needs of the individual.

Most metabolic behaviour of animals, i.e. organisms that live off other organisms, can be understood using a single reserve, but autotrophs, which obtain nutrients independently from the environment, require the delineation of more reserves, as will be discussed in Chapter 5.

1.1.4 Metabolic switching is linked to maturation

Metabolic switches occur, for instance, at the start of development of an individual, the moment at which age is initiated in DEB theory. Another switch occurs when assimilation is initiated, a moment called birth, or when allocation to maturation is redirected to reproduction, a moment called puberty, or when cell division occurs or at which DNA duplication is initiated. The age at which such switches occur differs widely among individuals of the same species, depending on the food uptake in the past. The size at which the switches occur differs already much less, but still shows some scatter.

DEB theory links the occurrence of such metabolic switches to the level of maturity, i.e. the set of regulation systems that control metabolic performance. Although allocation to reproduction does not occur as long as maturity is still increasing, this does not imply that maturity directly relates to preparation of the reproductive machinery only. I see maturity as a much more general investment to prepare the body for the adult state, which involves, among other things, extensive gene regulation switching and cell and tissue differentiation. Its formal status is information, not energy, mass or entropy. The building up of maturity costs energy, and maturity is quantified as the cumulated energy or amount of reserve that is invested in maturity. After being used to build up maturity, this energy becomes lost. Maturation can be conceived as metabolic learning and can be compared with reading a book or a newspaper; this costs considerable energy but forgetting the information does not give an extra release of heat or an extra carbon dioxide emission.

In multicellular organisms birth typically precedes puberty, which naturally leads to three life-stages: embryo, juvenile and adult.

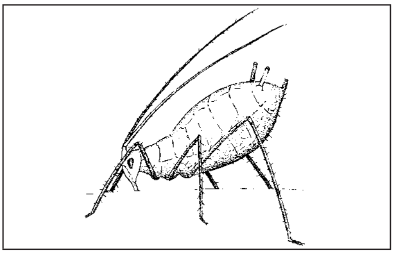
Embryo

The first stage is the embryonic one, which is defined as a state early in the development of the individual, when no food is ingested. The embryo relies on stored energy supplies. Freshly laid eggs consist, almost entirely, of stored energy, and for all practical purposes the initial structural volume of the embryo can realistically be assumed to be negligibly small. At this stage it hardly respires, i.e. it uses no dioxygen and does not produce carbon dioxide. (The shells of bird eggs initially produce a little carbon dioxide [125, 469].) In many species, this is a resting stage. This especially holds for plants, where seeds are equivalent to eggs; seeds can be dormant for many years and the number of dormant seeds greatly exceeds the number of non-dormant individuals [462]. Many seeds (particularly berries) require to be treated by the digestive juices of a particular animal species for germination; others need fire, see {428}. Although the seed or egg exchanges gas and water with the environment, it is otherwise a rather closed system.

Foetal development represents a variation on embryo development, where the mother provides the embryo with reserve material, such as in the Placentalia, some species of velvet worm *Peripatus* and the Devonian placoderm *Materpiscus* [717]. Complicated intermediates between reproduction by eggs and fetuses exist in fish [956, 1275, 1276], reptiles and amphibians [110, 899, 1112]. The evolutionary transition from egg to foetal development occurred several times independently. From the viewpoint of energetics, fetuses are embryos because they do not take food. The digestive system is not functional and the embryo does not have a direct impact on food supplies in an ecological sense. The crucial difference from an energetics point of view is the supply of energy to the embryo. In lecithotrophic species, nutrients are provided by the yolk of the ovum, whereas in matrotrophic species nutrients are provided by the mother as the foetus grows, not just in vitellogenesis. The fact that eggs are kept in the body (viviparity) or deposited in the environment (oviparity) is of no importance from an energetic perspective. (The difference is important in a wider evolutionary setting, of course.) As in eggs, a number of species of mammal have a developmental delay just after fertilisation, called diapause [1052].

Juvenile

The second stage in life history is the juvenile one, in which food is taken but resources are not yet allocated to the reproductive process. In some species, the developing juvenile takes a sequence of types of food or sizes of food particles. Most herbivores, for instance, initially require protein-rich diets that provide nitrogen for growth, see {185}. Some species, such as *Oikopleura*, seem to skip the juvenile stage. It does not feed as a larva, a condition known as lecithotrophy, and it starts allocating energy to reproduction at the moment it starts feeding. A larva is a morphologically defined stage, rather than an energy defined one. If the larva feeds, it is treated as a juvenile; if not, it is considered to be an embryo. So, the tadpole of the gastric-brooding frog *Rheobatrachus*, which develops into a frog within the stomach of the parent, should for energy purposes be classified as an embryo, because it does not feed. The switch from feeding to non-feeding as a larva seems to be made easily, from an evolutionary perspective. Sea urchins have developed a complex pattern of species that do or do not feed as a larva, even within the same genus, which comes with dramatic differences in larval morphology [1277, 1278, 1279]. Sperm of the sea urchin *Heliocidaris tuberculata*, which has feeding larvae, can fertilise eggs of *H. erythrogramma*, which has non-feeding larvae; the zygote develops into feeding hybrid larvae that resemble starfish larvae, similar to that of the distant ancestor of sea urchins and starfishes, some 450 Ma ago [928].



Parthenogenetic aphids have a spectacular mode of reproduction: embryos producing new embryos [596], see {358}. Since aphids are ovoviviparous, females carry daughters and granddaughters at the same time. From a formal point of view, the juvenile period is negative; the embryonic stage overlaps with the adult one. Aphids illustrate that the metabolic events of switching on feeding and reproduction matter, rather than the stages.

The word 'mammal' refers to the fact that the young usually receive milk from the mother during the first stage after birth, called the baby stage. Pigeons, flamingos and penguins also do this. The length of the baby stage varies considerably. If adequate food is available, the guinea-pig *Cavia* can do without milk [1052]. At weaning the young experience a dramatic change in diet, and after weaning the growth rate frequently drops substantially. Few biochemical transformations are required from milk to building blocks for new tissue. The baby, therefore, represents a transition stage between embryo and juvenile. The baby stage relates to the diet in the first instance, see {185}, and not directly to a stage in energetic development, such as embryo and juvenile. This can best be illustrated by the stoat *Mustela erminea*. Although blind for some 35–45 days, the female offspring reaches sexual maturity when only 42–56 days of age, before they are weaned. Copulation occurs whilst they are still in the nest [597, 1052].

Asexually propagating unicellular organisms take food from their environment, though they do not reproduce in a way comparable to the production of eggs or young by most multicellular organisms. For this reason, I treat them as juveniles in this energy-based classification of stages. Although I realise that this does not fit into standard biological nomenclature, it is a logical consequence of the present delineations. I do not know of better terms to indicate energy-defined stages, which highlights the lack of literature dealing with the individual-based energetics of both micro- and multicellular organisms. This book shows that both groups share enough features to try to place them in a single theoretical framework. Some multicellular organisms, such as some annelids, triclads and sea cucumbers (e.g. *Holothuria parvula* [323]), also propagate by division. Some of them sport sexual reproduction as well, causing the distinction between both groups to become less sharp and the present approach perhaps more amenable.

The eukaryotic cell cycle is usually partitioned into the interphase and mitotic phases; the latter is here taken to be infinitesimally short. The interphase is further decomposed into the first gap-phase, the synthesis phase (of DNA) and the second gap-phase. Most cell components are made continuously through the interphase, so that this distinction is less relevant for energetics. The second gap-phase is usually negligibly short in prokaryotes. Since the synthesis phase is initiated upon exceeding a certain cell size, size at division depends on growth conditions and affects the population growth rate. These phenomena are discussed in some detail on {279}.

In many species, the switch from the juvenile to the adult stage is hardly noticeable, but in the paradoxical frog, for instance, the switch comes with a dramatic change in morphology and a substantial reduction in size from 20 to 2 cm; the energy parameters

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differ between the stages. Holometabolic insects are unique in having a pupal stage between the juvenile and adult ones. It closely resembles the embryonic stage from an energetics point of view, see {284}. Pupae do not take food, and start synthesising (adult) tissue from tiny imaginal disks. A comparable situation occurs in echinoderms, bryozoans, sipunculans and echiurans, where the adult stage develops from a few undifferentiated cells of the morphologically totally different larva. In some cases, the larval tissues are resorbed, and so converted to storage materials; in other cases the new stage develops independently. When *Luidia sarsi* steps off its bipinnaria larva as a tiny starfish, the relatively large larva may continue to swim actively for another 3 months, [1136] in [1257]. Some jelly fishes (Scyphomedusae) alternate between an asexual stage, i.e. small sessile polyps, and a sexual stage, i.e. large free-swimming medusae. Many parasitic trematodes push this alternation of generations to the extreme. Mosses, ferns and relatives alternate between a gametophyte and a sporophyte stage; the former is almost completely suppressed in flowering plants. From an energetics perspective, the sequence embryo, juvenile is followed by a new sequence, embryo, juvenile, adult, with different values for energy parameters for the two sequences. The coupling between parameter values is discussed on {295}.

Adult

The third stage is the adult one, in which energy is allocated to the reproduction process. The switch from the juvenile to the adult stage, puberty, is here taken to be infinitesimally short. The actual length differs from species to species and behavioural changes are also involved. The energy flow to reproduction is continuous and usually quite slow, while reproduction itself is almost instantaneous. This can be modelled by the introduction of a buffer, which is emptied or partly emptied upon reproduction. The energy flow in females is usually larger than that in males, and differs considerably from species to species.

Some Florideophyceae (red algae) and Ascomyceta (fungi) have three sexes; most animals and plants have two, male and female, but even within a set of related taxa, an amazing variety of implementations can occur. Some species of mollusc and annelid, and most plants, are hermaphroditic, being male and female at the same time; some species of fish and shrimp are male during one part of their life and female during another part; plants such as the bog myrtle *Myrica gale* can change sex yearly; some have very similar sexes while other species show substantial differences between males and females; see Figure 1.1. The male can be bigger than the female, as in many mammals, especially sea elephants, or the reverse can occur, as in spiders and birds of prey. Males of some fish, rotifers and some echiurans are very tiny, compared to the female, and parasitise in or on the female or do not feed at all. The latter group combines the embryo stage with the adult one, not unlike aphids. Differences in ultimate size reflect differences in values for energy parameters, see {299}. Parameter values, however, are tied to each other, because it is not possible to grow rapidly without eating a lot (in the long run). Differences in energy budgets between sexes are here treated in the same way as differences between species.

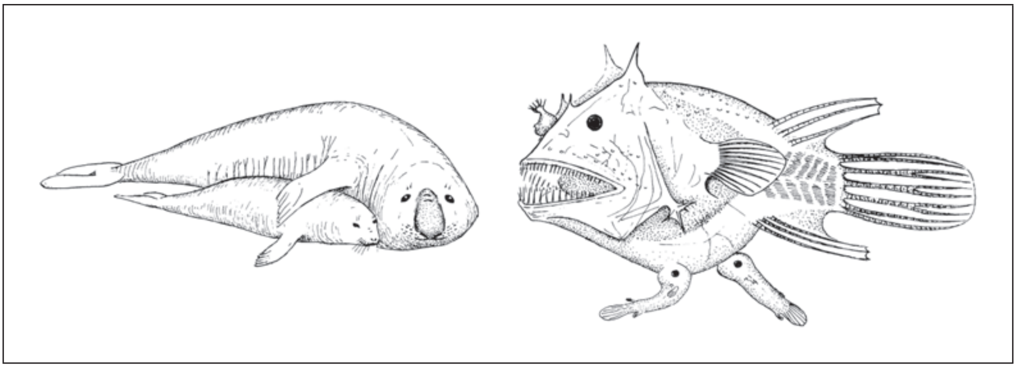
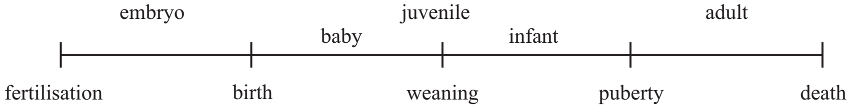


Figure 1.1 Sexual dimorphy can be extreme. The male of the southern sea elephant *Mirounga leonina* is 10 times as heavy as the female, while the parasitic males of the angler fish *Haplophryne mollis* are just pustules on the female's belly.

Reproduction, in terms of the production of offspring, does not always have a simple relationship with gamete production. All oocytes are already present at birth for future ovulations in birds and mammals, where they are arrested at prophase I of meiosis [798] (which occurs at the transition from the second gap-phase to the mitotic phase). In some species of tapeworm, wasp and at least 18 species of mammal (e.g. armadillo) there is a mode, called polyembryony, in which a sexually produced embryo splits into several genetically identical offspring. The opposite also occurs in several species of mammal (e.g. pronghorn, elephant shrews, bats, viscacha), where the mother reduces a considerable number of ova to usually two, early in the development, but also later on, by killing embryos [108]. Cannibalism among juveniles inside the mother has been described for *Salamandra*, some sharks and the sea star *Patiriella* {185}. Parent coots, *Fulica*, are known to drown some hatchlings of large litters, possibly to increase the likelihood of the healthy survival of the remaining ones.

In some species, e.g. humans, a senile stage exists, where reproduction diminishes or even ceases. This relates to the process of ageing, see {214}. An argument is presented for why this stage cannot be considered as a natural next stage within the context of DEB theory.

The summary of the nomenclature used here reads:



1.2 Homeostasis is key to life

Homeostasis is the ability to run metabolism independent of the (fluctuating) environment. All living systems do this to some extent and to capture this extent DEB theory makes use of several homeostasis concepts, which are discussed in this section.

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The compounds that cells use to drive metabolism require enzymes for their chemical transformation. Compounds that react spontaneously are excluded or stored such that this cannot occur. In this way cells achieve full control over all transformations, because they synthesise enzymes, consisting of protein, themselves. No reaction runs without the assistance of enzymes. The properties of enzymes depend on their micro-environment. So homeostasis is essential for full control. Changes in the environment in terms of resource availability, both spatial and temporal, require the formation of reserve pools to ensure a continuous supply of essential compounds for metabolism. This implies a deviation from homeostasis for cells (or individuals) as a whole. The cell's solution to this problem is to make use of polymers that are not soluble. In this way these reserves do not change the osmotic value, and neither do they affect the capacity of monomers to do chemical work (see {79}). In many cases cells encapsulate the polymers in membranes, to reduce interference even further, at the same time increasing access, as many cellular activities are membrane bound.

1.2.1 Strong homeostasis: stoichiometric constraints

The chemical composition in small volumes, such as in bacterial cells and eukaryotic cell compartments is intrinsically stochastic, see {430}, and therefore fluctuates. So homeostasis is never perfect. DEB theory assumes that the chemical composition of reserve(s) and structure(s) are constant, an assumption called the strong homeostasis assumption. The basic idea is to delineate enough reserve(s) and structure(s) to approximate this situation, but for animals a single reserve and a single structure already captures most variation in the chemical composition of biomass, mainly because the variation in the chemical composition of their food is limited. The amounts of reserve(s) and structure(s) can vary, but not their chemical composition. The mixture of chemical compounds that make up these pools can, therefore, be considered as a single generalised compound.

To produce a compound of constant chemical composition, substrates for this production are required in particular relative amounts, which gives what is called stoichiometric constraints on production. A lot of ecological literature focuses on the availability of chemical elements [1110], but the production is from chemical compounds, however, not from chemical elements directly and the problem is that compounds can be transformed into other compounds, which complicates matters considerably. Primary production on Earth is mainly limited by nitrogen, for instance, while 70% of the atmospheric gases consist of dinitrogen; only a few organisms can use this nitrogen, however. The problem of specifying the constraints on production is one of the main tasks of DEB theory, which is a rather complex one because some compounds can partly replace others.

Reserve materials can be distinguished from materials of the structural mass by a change in relative abundance if resource levels change. This defining property breaks down in case of extreme starvation, when structural materials are degraded as well when reserves are exhausted. An example of this is the breakdown of muscle tissue during extreme starvation. Even if food intake is resumed, the structural component of muscle tissue does not recover in mammals such as ourselves.

Since the amount of reserves can change relative to the amount of structural material, the chemical composition of the whole body can change. That is, it can change in a particular way. This is a consequence of choosing energy as a state variable rather than the complete catalogue of all compounds.

1.2.2 Weak homeostasis: restrictions on dynamics

DEB theory also uses another homeostasis assumption: weak homeostasis. Its definition is that *if food density does not change* reserve density, i.e. the ratio between the amounts of reserve and structure, becomes constant *even when growth continues*; reserve and structure grow in harmony and biomass no longer changes in composition. This makes sense only if reserve and structure obey strong homeostasis, so weak homeostasis implies strong homeostasis, but is more restrictive. The fact that growth still can continue is essential for the weak homeostasis concept. Weak homeostasis applies to the whole body, not to its compartments, but under steady-state conditions only. Strong homeostasis has nothing to do with reserve dynamics, but weak homeostasis turns out to fully determine reserve dynamics, see {38}.

1.2.3 Structural homeostasis: isomorphy

Structural homeostasis is about shapes, not about chemical composition. For an understanding of energetics, only two aspects of size and shape are relevant, as is explained later: surface areas for acquisition processes and volumes for maintenance processes. The shape defines how these measures relate to each other. If an individual does not change in shape during growth, it is called an isomorph. Isomorphism is an important property that applies to the majority of species on Earth by approximation. The shape can be any shape and the comparison is only between the shapes that a single individual takes during its development. If organisms have a permanent exoskeleton, however, there are stringent constraints on their shape [637].

Two bodies of a different size are isomorphic if it is possible to transform one body into the other by a simple geometric scaling in three-dimensional space: scaling involves only multiplication, translation and rotation. This implies, as Archimedes already knew, that if two bodies have the same shape and if a particular length takes value L_1 and L_2 in the different bodies, the ratio of their surface areas is $(L_1/L_2)^2$ and that of their volumes $(L_1/L_2)^3$, irrespective of their actual shape. It is, therefore, possible to make assertions about the surface area and the volume of the body relative to some standard, on the basis of lengths only. One only needs to measure the surface area or volume if absolute values are required. This property is used extensively in this book.

Structural homeostasis is an assumption of the standard DEB model, but not of DEB models generally. Notice that length itself does not play a role in DEB theory and everywhere where it occurs while isomorphy is assumed, length actually stands for the ratio of volume and surface area. Section 4.2 at {124} considers changes in shape and its consequences for energetics.