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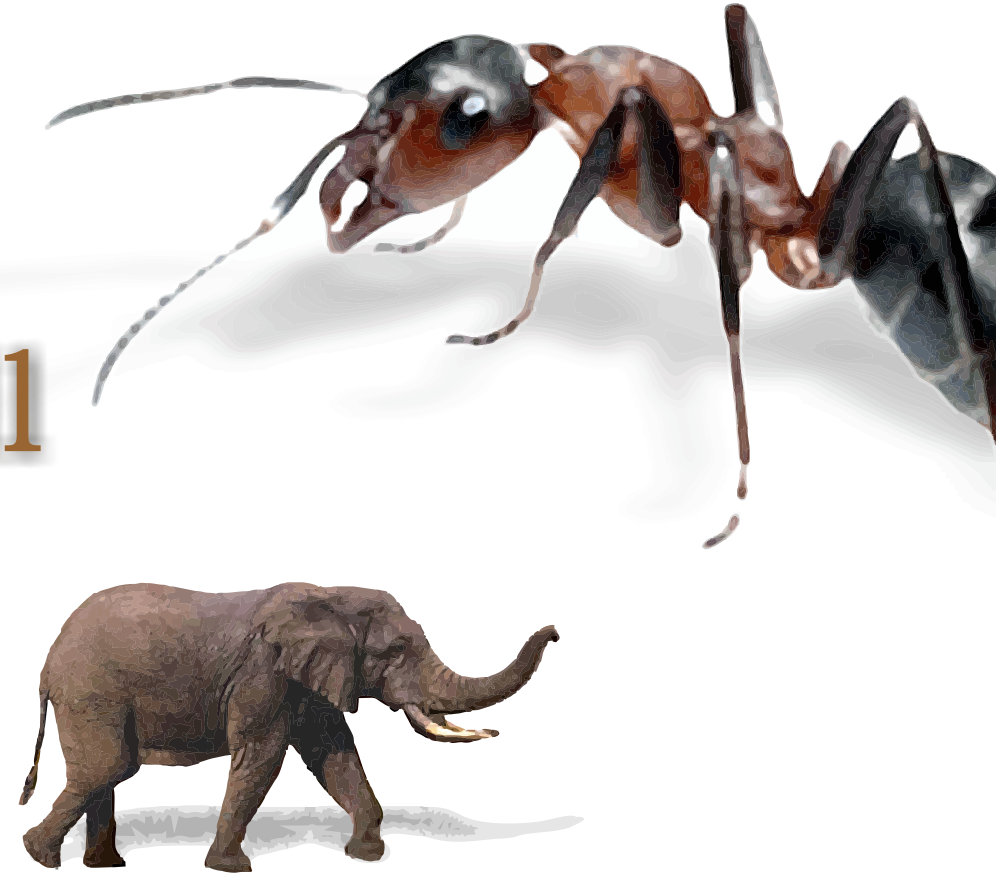

Jan Marcin Węsławski & Dag O. Hessen

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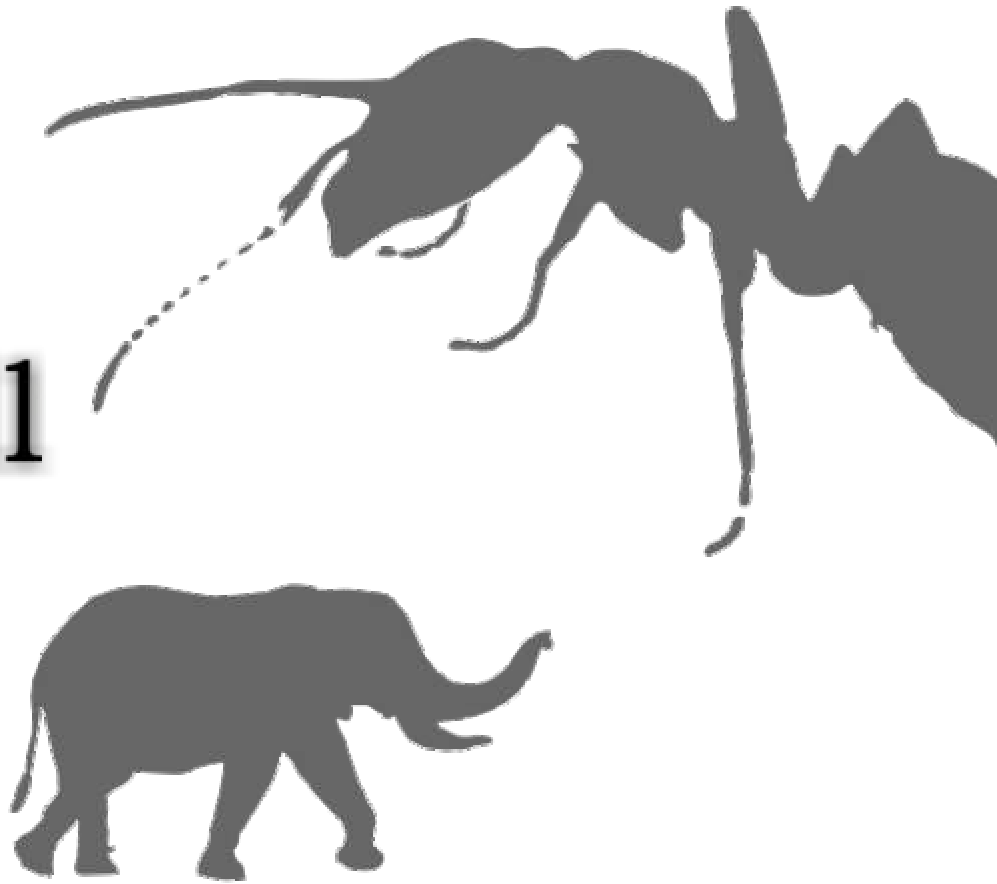

Jan Marcin Węsławski & Dag O. Hessen

DWARF

Declining size – a general response to climate warming in Arctic fauna?

Project funded by Norwegian Funding Mechanism in 2013 nr DZP/POL-NOR/201992/93/2014

main message

Body size is a fundamental biological unit that is closely coupled to key ecological properties and processes. Decline in organisms' body-size has been recently predicted to be the third universal biological response to global warming (alongside changes in phenology and distribution of species) in both aquatic and terrestrial systems. The main goal of the project is to test hypothesis that elevated temperatures will induce size reductions in a large range of animals in the Arctic. The natural selection towards smaller forms in warming Arctic may have a far-reaching influence on the high latitude ecosystems functioning, especially the food web dynamics and carbon cycle.

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Introduction

Size of organism varies tremendously, but why? Size is one of the most important properties of a species and individual organisms, and has important implications for ecology and evolution. Size determines to a large extent who eats whom, but size come also with costs. Being large may imply that there are fewer enemies, but large bodies needs lots of energy. Also within species size may vary substantially. Individual life history and access to food and environmental conditions, dictates if one individual grows large and other from the same population remains small. On the scale of community, the proportion between small and large species tells the difference about the resources use. Furthermore, as the size of animals also is flexible and depends on the environmental conditions, it may change in response of ambient conditions. As global temperature is rising, it is important to understand how this will affect ecosystems, including size of organisms.

Arctic ecosystems is currently experiencing rapid warming, and this also holds for marine ecosystems. In this booklet we will look into the fascinating phenomenon of body size in animals. Notably we will relate such gradients from south to north, and discuss the main drivers and rules that are responsible for the size of organisms, and how this may be affected by climate change.

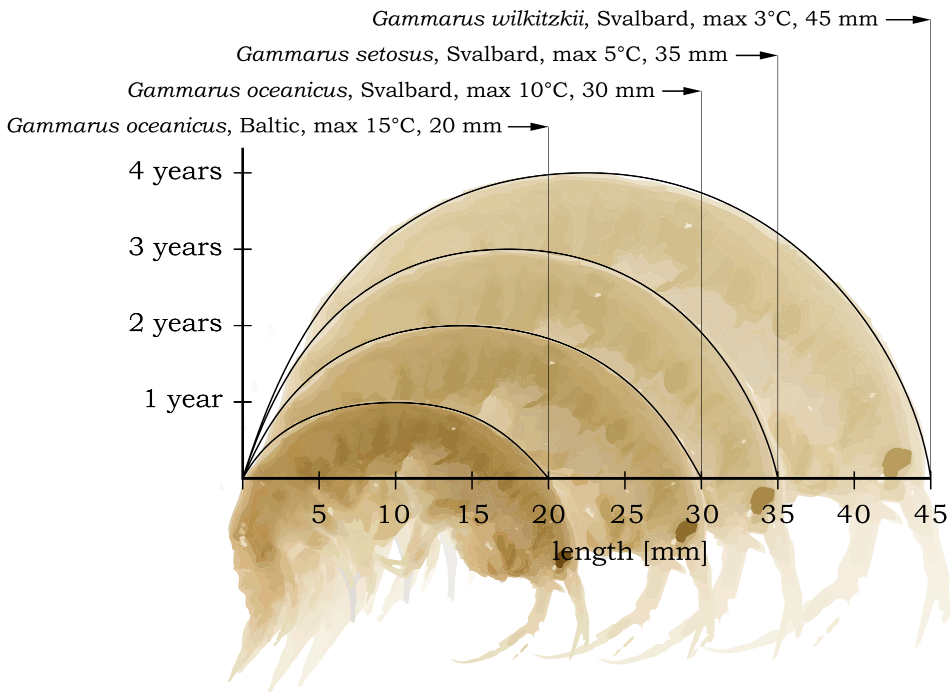


Fig. 1 Similar species use to be small in warm areas and large in cold waters. Here the crustacean - *Gammarus.*

Size in organisms

Animals and plants can either consist of one single cell, or being composed of multiple cells. We think of single-celled organisms as tiny and microscopic, and indeed they are, but even within the world of unicellular species, like phytoplankton, there is a tremendous variability is size. E.g. from the tiniest cyanobacteria (bluegreen bacteria doing photosynthesis just like algae) to the very largest cells, cover a 250 000 times size span, from ca 0.2 µm (1 µm = 0.0001 cm or 0.001 mm) to 5 cm (the bubble algae *Valonia ventriculosa*). Within phytoplankton, the largest cells may reach size of 2 mm which still is a size span of 10 000. Also unicellular animals cover an almost similar size span, and when mowing to the multicellular animals, we encounter an even larger size span, from organisms such as tiny rotifers of e.g. 0.3 mm to the largest blue-whale of 30 m is a span of 100 000. All whales are large and all copepods are small, but still within the copepods and whales there is a 10 times size span. For fish there is even a larger span, from dwarfed fish of only a few millimetres as adults, to the whale-shark of up to 12 meters. So why do animals (or plants for that matter) differ so tremendously in size? Is there a simple explanation, or multiple explanations? And do we really know why? All organisms are shaped by their evolution, so the short answer is that size is an adaptation to the challenges in life, but that also means that there are multiple ways of solving the key drivers in evolution: eat, survive and reproduce.

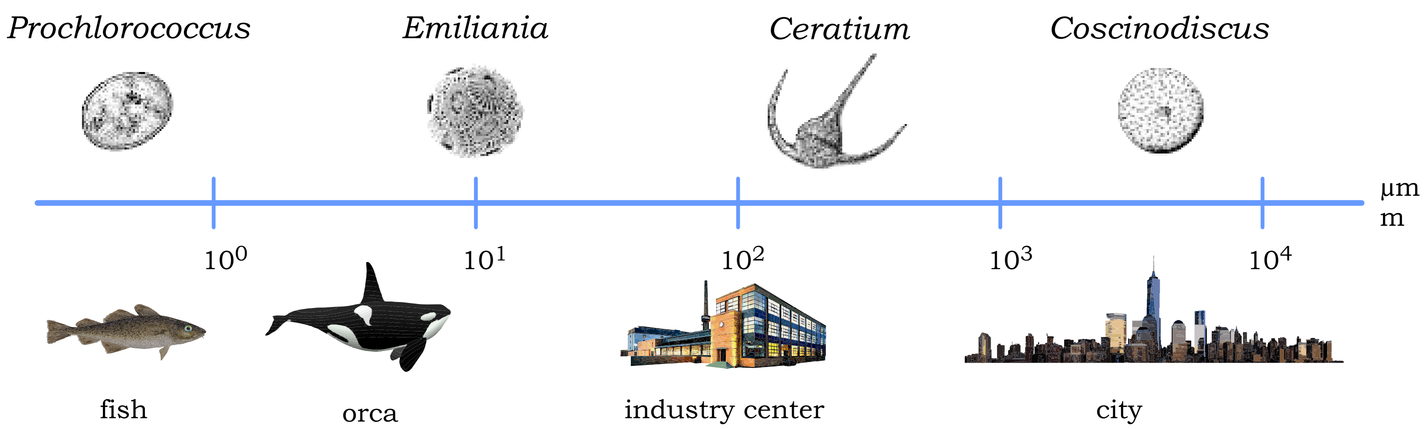


Fig. 2 Comparision of scales span among unicellular organisms (above the bar) and macro-objects (below the bar).

Table 1. Smallest and largest animals in selected taxa.

Unit	**Metric value**	**Example of organisms**
Tens of meters	10	Whales
Meters	1	Pinnipeds, fish
Centimeters	10^{-2}	Crustaceans and insects
Millimeters	10^{-3}	Small benthos, plankton
Microns	10^{-6}	Meiofauna
Nanometers	10^{-9}	Microplankton, flagellates
Picometers	10^{-12}	Picoplankton, bacteria, blue green algae

What is the span between large and small animals in water and on land?

Size among the homeotherm species (birds and mammals – that can sustain stable body temperature) is differently distributed among marine and terrestrial species. The aquatic mammals are large or very large – the smallest marine mammals are sea otters or hawaiian seals of about 1 m length and weights of several kilo. The terrestrial mammals on the contrary are dominated by small species like rodents or insectivores, with the smallest known mammal, the Etruscan shrew, being only 2 g (Table 2).

The main reason for this difference is the exceptional feature of water – its heat content. Water, contrary to air, is difficult to warm up and it gives the heat away very slowly. It means that heat loss in the water is 25 times faster than in the air – so to keep your body warm in water, you need to be very well isolated (like blubber layer in seals) and be voluminous to prevent the heat loss. Such as the pinnipeds, dolphins and whales, big enough to keep the body warm efficiently in the water. The only known homiothermic fish are large tuna species- they occur in warm waters, and need homiothermy to maintain high speed, that can be achieved with a large body only. On land the small mammal (especially in warmer climate) can do well, so land animals are dominated by small species like rodents, insectivores and small carnivores (Fig. 3).

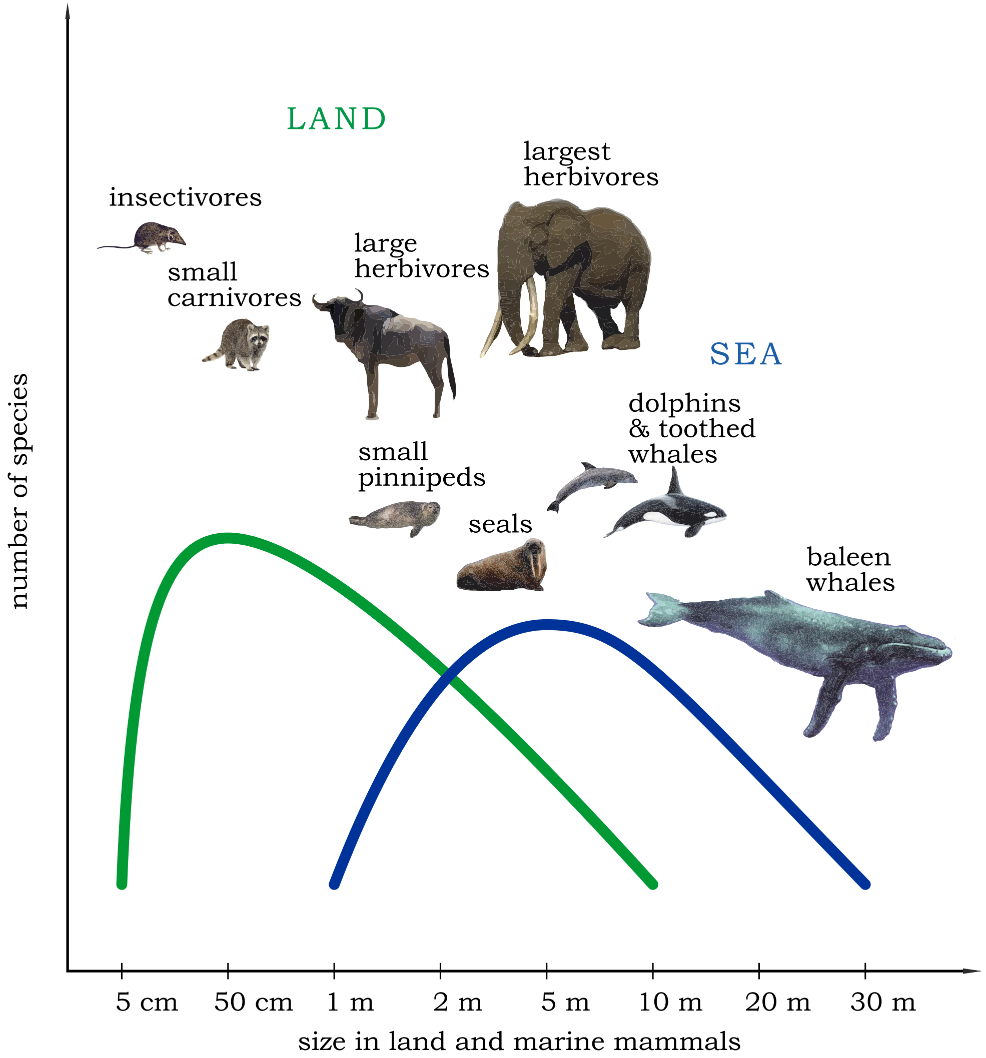


Fig. 3 Distribution of size in land and aquatic mammals.

The minimal body size in warm blooded animals is dictated by heat loss control. There are many constraints on body size are - and again species on land or in water respond differently to these challenges.

Another property of water is that it reduced weight, meaning that heavy weight is easy to carry. Gravity limits the upper animal size on land – you may not sustain the soft body like a giant squid and be a terrestrial animal. The large weight needs water drag to keep the body cavities and to maintain its movement. Inner skeleton is the best option up to a certain size (elephants, while for even larger bodies the best solution was) to move into the water (as whales did). The largest dinosaurs probably lived partly emerged in water, and this is also why blue-whale, the largest creature that ever has lived on earth, is aquatic.

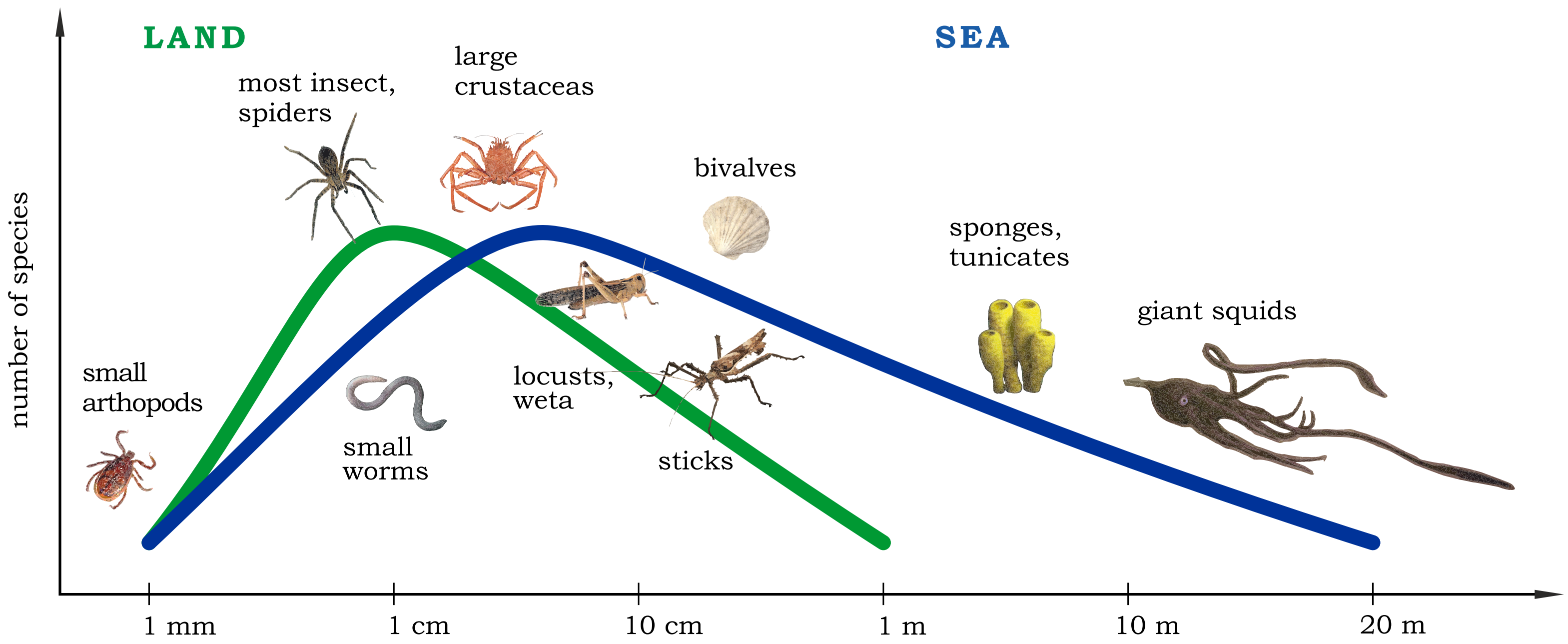


Fig. 4 Distribution of size in land and aquatic invertebrate species.

Table 2. Smallest and largest animals in selected taxa.

Taxon	Smallest species	Size	Geographic area, habitat	Largest species	Size	Geographic area, habitat
Fish	*Paedocypris progenetica*	8 mm	Indonesia, warm, fresh water	*Mola mola* (Sunfish)	4 m diameter, 2300 kg	Tropical open ocean
Mammals	*Suncus etruscu* (Etruscan shrew)	2 g	Dry, subtropics	*Balaenoptera musculus* (Blue whale)	30 m, 190 tonn	Open ocean
Crustaceans	*Stygotantulus stocki* (amphipod)	0.1 mm	Epiparasite, littoral, Atlantic	*Pseudocarcinus gigas* (crab)	13 kg, 50 cm	Australian sublittoral
Molluscs	*Truncatella* sp. (shell gastropod)	2 mm	Tropical, littoral Atlantic	*Architeuthis dux* (Giant squid)	18 m, 900 kg	Abyssal open ocean

If we look at the smaller animals, the invertebrates (without inner skeleton, but with external shells or armor only) are all surprisingly small. The largest insect is only about 60 cm in length, the heaviest land arthropod is the coconut crab which in fact can reach the impressive weight of 4 kg, but by and large land is frequented with small species (between few mm and few cm) as presented on Fig. 4. The reason why we do not see horse-sized (or dog-sized for that matter) insects is related to some physiological constraints as explained below.

With the help of buoyancy in the water, the gravity limitation is not that important, soft-bodied marine invertebrates may grow very large – like a giant squid (up to 20 m length) or sponges (few meters in diameter). The largest bivalves are about 1m size, and longest worms reach of few meters length – the giant Australian earthworm is in fact an aquatic animal as it lives in the holes filled with the water.

What are the physical limitations to the size of an organism.

The gravity on land pose a problem for large animals, they need to overcome collapse and to transport fluids to distant parts of the body. In trees the trunk diameter is directly responsible for the possible height of the specimen – and such relation was described centuries ago. The tallest trees may withstand strong winds with massive trunks and roots, while the transportation of fluids and nutrients from the soil to the crown becomes a challenge. Comparative anatomy shows that bones and muscles of large and small animals are very similar in their structure and efficiency. To a large extent the volume of muscle and diameter of the bone increases with an animal size. So the mouse and elephant bones are similar, considering the weight difference. This implies that there is a limit to the size of the land animal – related to its feeding and mobility mode. Herbivore animals (those eating grass and other plant material) have plenty of food and may also grow large. Since plant food is of low nutritional value, they need to eat almost constantly, and they also need large gut and efficient digestive systems to process all this low-quality food. This is one reason why herbivore mammals often are large. Furthermore, the larger the herbivore grow, the easier it is to escape the predators, but there is an upper limit to size partly due to food demands (a big elephant may need 400 kg of food every day) and partly due to weight. For most of aquatic organisms the weight is not really an issue, as their body cavities are filled with water, and water is not compressible. Huge pressure in the deepest ocean canyons, does not affect organism, as long as they are adopted to the depth. On the other hand most of deep water organisms are small, which is an effect of food scarcity in the deep and dark waters.

Temperature exchange is very important in the context of animal size. Heat loss is directly related to the body area (as the heat escapes through the skin) and inversely to the body volume (larger bodies have slower heat loss). This is why large animals may live in cold climate, and small animals like minute rodents and hummingbirds preventing the heat loss need to run instantly after the food and may not slow down. The shape of the organism is also important, the more rounded the body, the lower the heat loss, while all extensions like ears, long neck or slender legs help in heat removal in hot climate (compare the polar and desert fox – Fig. 5). More recent examples of temperature related changes in mammals size are from squirrels, gophers and woodrats – the sizes diminished following the change from cold XIX century "little ice age" to present day warming.

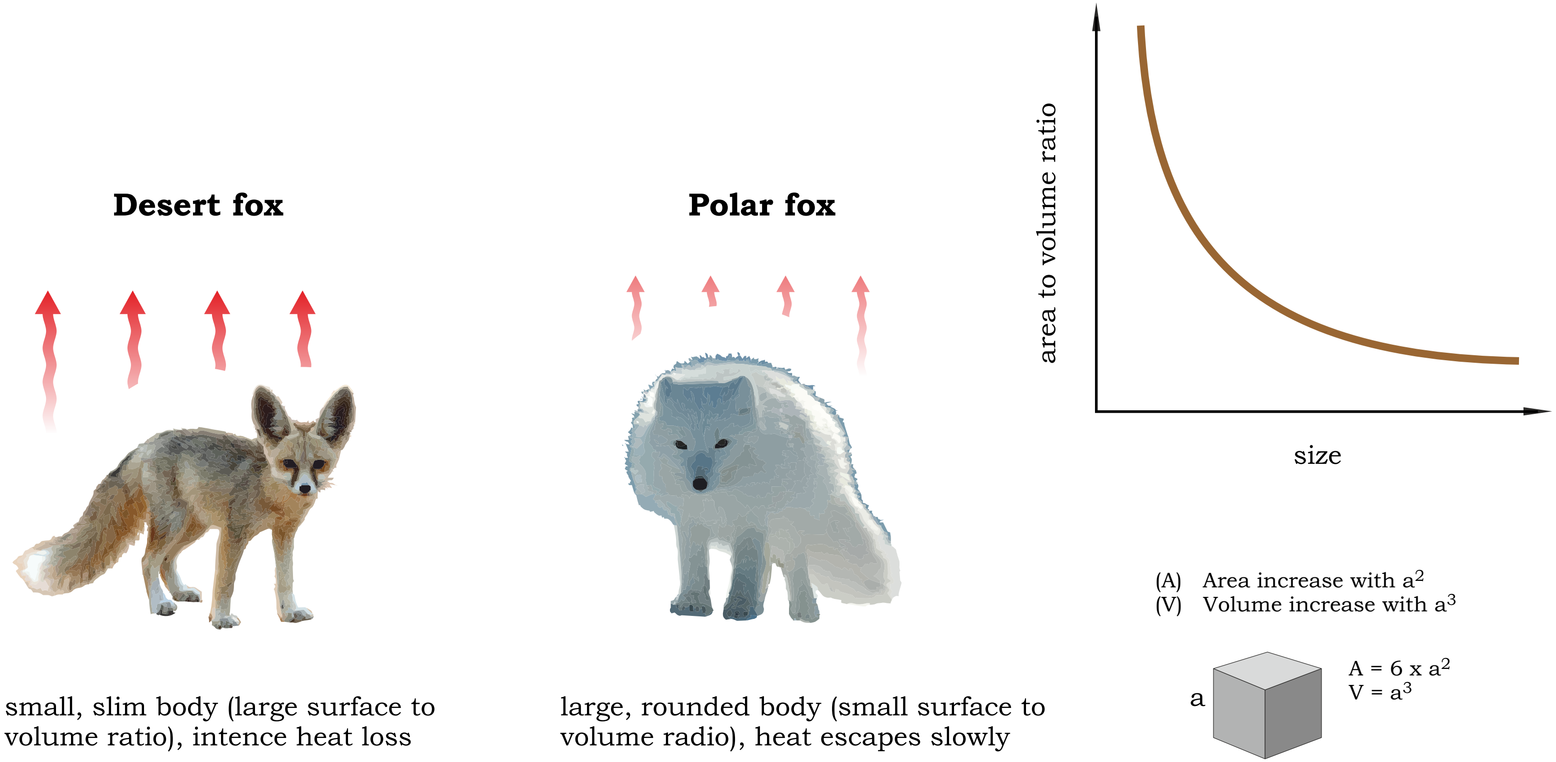


Fig. 5 Size and rate of heat exchange between homeothermic organism and environment.

Time and space – relation to the organism size

All the reactions (like biochemical synthesis) or processes (like rate of diffusion) take time, and when it occurs on the unicellular level these reaction might be very swift – like time of nutrients penetration through the cell wall. In larger organisms the same process is multiplied by the size – the way the molecule need to cover to its destinations.

The smaller the aquatic organisms are, the more important is the viscosity of water, and less important is the shape of the organism (rounded and elongated). For larger organisms like fish, a streamlined shape is helpful. Water offer resistance. What looks like a very rapid movement of an microbe in water droplet under the microscope, is in fact slow compared to larger organisms moving in the air.

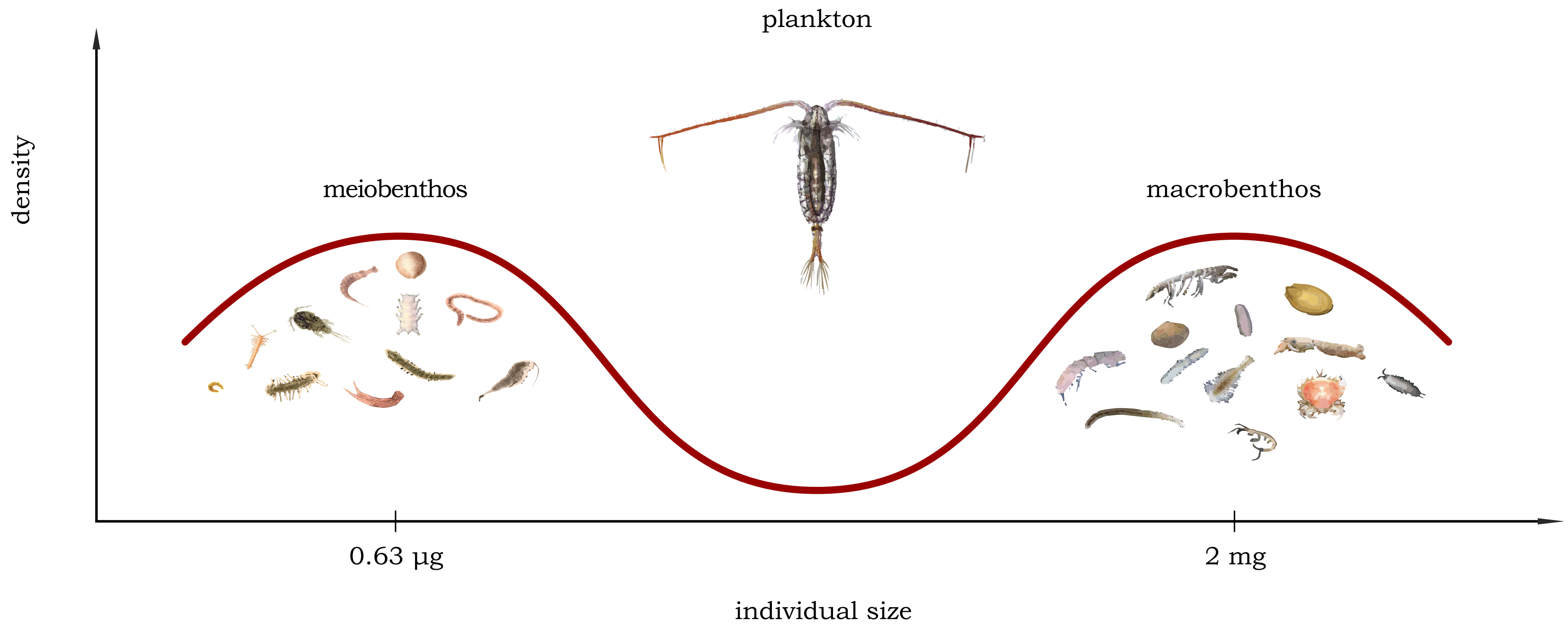


Fig. 6 Characteristic distribution of size in marine organisms – most of the planktonic organisms fit well in the gap between two dominant size groups of seabed fauna.

Mobility of organisms living on the sea-bed is clearly linked to their size. The smallest meiofauna species may swim among sand grains using the interstitial cavities, while the macrofauna is strong and large enough to push away the sediment, built holes and mounds. Throughout the climatic zones and depths, the size distribution of marine benthos shows the same pattern – namely two separate peaks representing meio- and macrofauna (Fig. 6). The gap between the two size groups fits the size of mesozooplankton – the most abundant organisms in the pelagic domain.

The species/area curve is an important ecological feature, that links the species diversity with the area of its distribution. In practical terms it means, that the larger area we sample (observe), the more species will be encountered. The slope of the species/area curve is strongly dependent on the size of the animals. Very small organisms are widespread, and can be found easily even on the small area. Larger species needs more space. The largest animals needs both the big amount of food and large area to forage. The largest carnivores use to have huge hunting grounds – for Polar bear it may be hundreds of km^2, have been (Fig. 7).

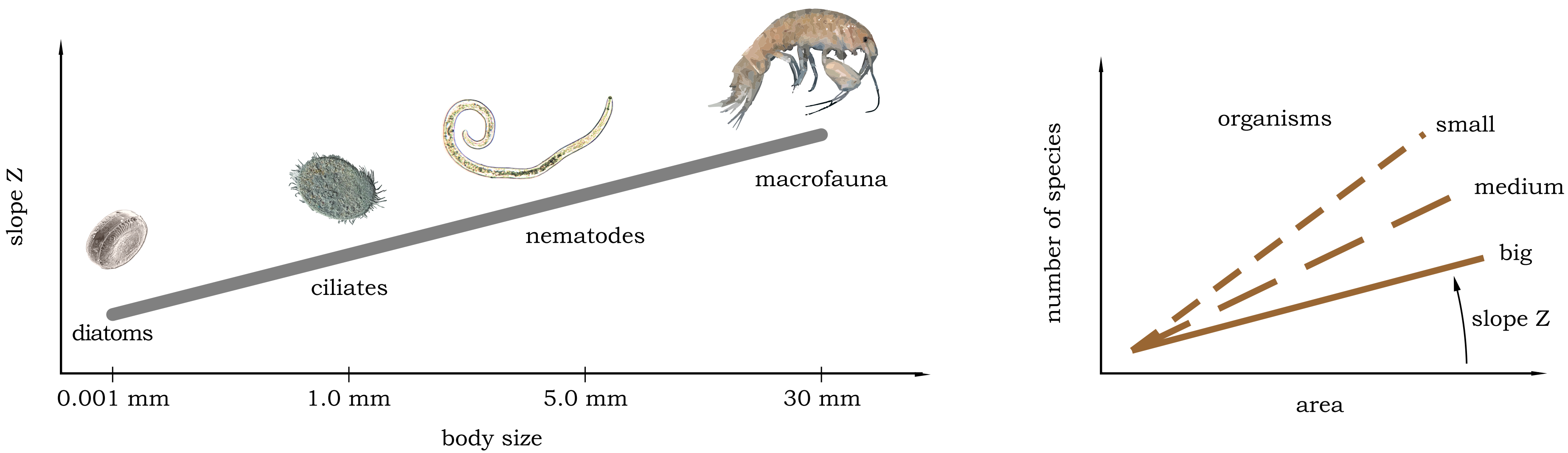


Fig. 7 The slope of the species –area relation and its dependence to the size of organisms.

Animal size and the food web

Size is often determining whether you are a prey (that gets eaten) or predator (that east other). Most animals are in fact both, but the larger you gets, the less likely is the chance of someone larger eating you (elephants and blue-whales are pretty safe for predators). But as we have seen, being large comes with costs, you need to eat a lot to obtain energy to your large body. Body size both for herbivores and carnivores (the predators) also determines what you can eat. While a copepod in the ocean may engulf its food (microscopic algae) whole, caterpillar larvae eat only pieces of single leafs while the elephant may eat large branches and whole shrubs.

As the animal size increases with growth its feeding abilities are also widens. Among marine crustaceans, small juveniles tend to be herbivores or bacterial feeders, larger ones and adults of the same species are carnivorous. The adults of the large species are much bigger from the juveniles, compared to such difference in small species. This leads to cannibalism and foraging on the variety of small and larger prey (expansion of the feeding niche). The size of the predator and its strategy – to be either opportunistic (takes any prey that can be collected) or selective (feeds only on the prey of certain size). This makes a difference for the population of prey – when the opportunistic predators prevail, the pressure is strongest on the smallest prey organisms (anyone can take them) and the small prey species dominate. When the selective predators dominate in the ecosystem, the pressure on the prey is spread evenly on different sizes of the prey, and larger prey species prevails (only largest predators can take them – Fig. 8).

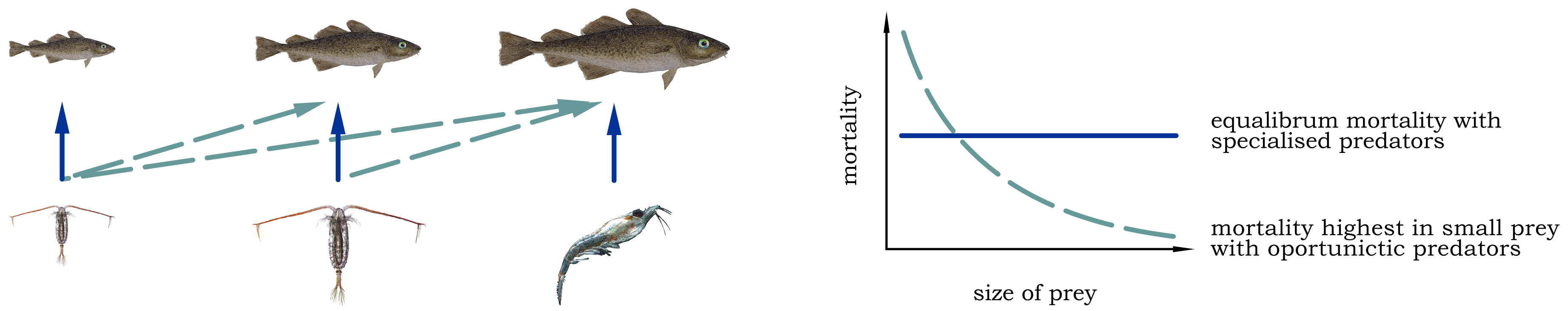


Fig. 8 Pressure on prey created by the size of carnivores (specialised or opportunistic) and the effect on the prey size structure.

A unique feature of the marine food web is that the primary production in open waters are run by microscopic plants (phytoplankton) that implies that even tiny herbivore may graze directly on microplankton, and consequently the small grazer, will be taken by small predator only. Contrary the large plants (grass, bush, trees) are less efficiently consumed by the herbivores. Human exploitation of terrestrial biological resources is very efficient – as we may consume either large primary producers (lettuce) or large grazers (cows). In the marine realm we exploits the large fish – top predators of the system – equivalent of lions and tigers on land, – and this implies a less efficient exploitation (Fig. 9). In cold water, the marine herbivores may grow exceptionally large – like krill and other macroplankton species of few centimeter length). This permits top predators, even large like seals or big birds to feed directly on low trophic level, and such linkage makes most efficient food web known from the sea. When and where the water gets warmer the smaller and more diverse organisms prevail and energy is dissipated in more complicated food web (Fig. 10).

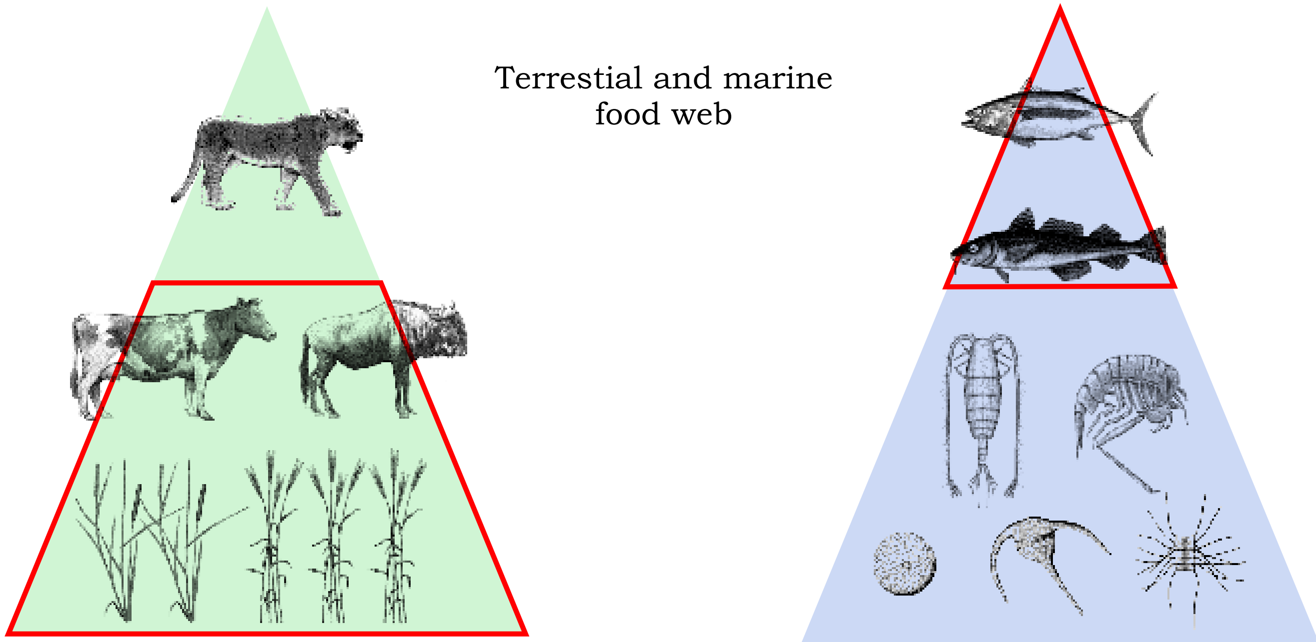
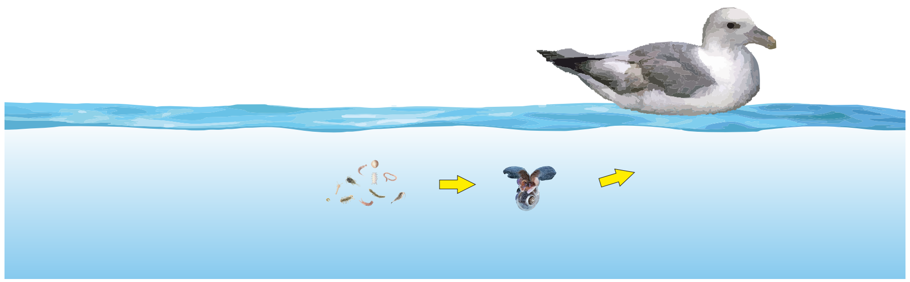
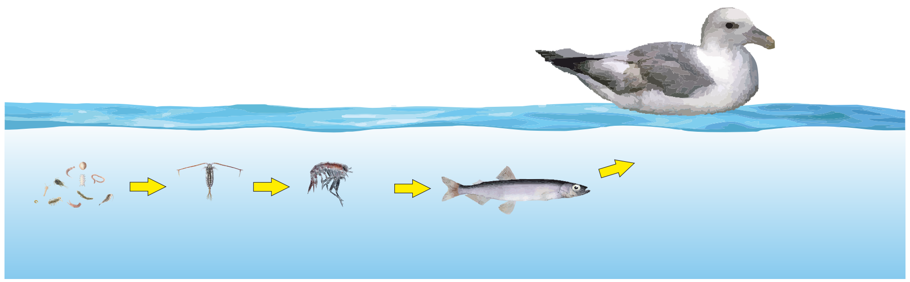


Fig. 9 Size of the marine and land grazers reflects the size of their food. Large plants can be a consumed directly by large herbivores, while microscopic phytoplankton can be absorbed by minute grazers only. Red lines indicates level exploited by man. In the terrestrial domain we are able to exploit the basis of the food web with small energy loss. In contrary, in the sea we are collecting the top predators with significant energy loss.



Low energy systems, production/biomass ratio decreases, slow growing, large organisms prevail.



High energy systems, production/biomass ratio increases, with dominance of small, fast growing organisms.

Fig. 10 The short food web in low energy systems (polar areas) exists, where in cold water, slow growing grazers may grow big enough (krill, pteropods) to be collected by top predators. In warmer waters, (high energy systems) pelagial is dominated with small, diversed organisms, energy is dissipated among numerous elements of the food web.

So far we have learned something about the ecological and evolutionary drivers behind small or large body size. There are strong differences between species and not the least type of species. Insects are really never large compared to the vertebrates (those that are stiffened up by an inner skeleton like ourselves), and invertebrates as well as vertebrates in the ocean tend to me much larger compared with those on land. We have also seen that this can be explained to a large extent by the physical properties of water. But what does really at the basal level constitute the difference between for example a mouse and an elephant. Is simply the mouse a downscaled version of an elephant – or vice versa?

Body size, cell size and genome size

All organisms are made up by cells, so does a mouse simply have fewer cells, or do they have much smaller cells than an elephant? For most mammals and birds, the answer is rather straightforward – small and large species differ primarily in cell numbers. This changes a bit when we move to the invertebrates which may differ strongly in cell size, and where cell size also in many cases scales with body size. However for both vertebrates and invertebrates, growth mainly occur by adding more cells. We all start our lives as a fusion of two cells, and as we grow, these cells specialize into tissues such as bone, muscles, liver, nerves, skin in increasing numbers until we reach our final body size.

Now, if we turn from differences in size between species or groups, to differences within species, it clearly makes a difference whether we consider newborn or adults, but species may also differ in size depending on their environment. Most invertebrates and other ectotherms (those with a body temperature reflecting the ambient) grow slower at low temperature because all processes slow down, but they may attain larger adult size. Particularly marine invertebrates that resides at large depths or in cold water may reach large sizes, sometimes very large sizes, compared to their southern counterparts. E.g. gigantic amphipods, starfish and sea-spiders may be found here, and interestingly they often have large cells. But why?

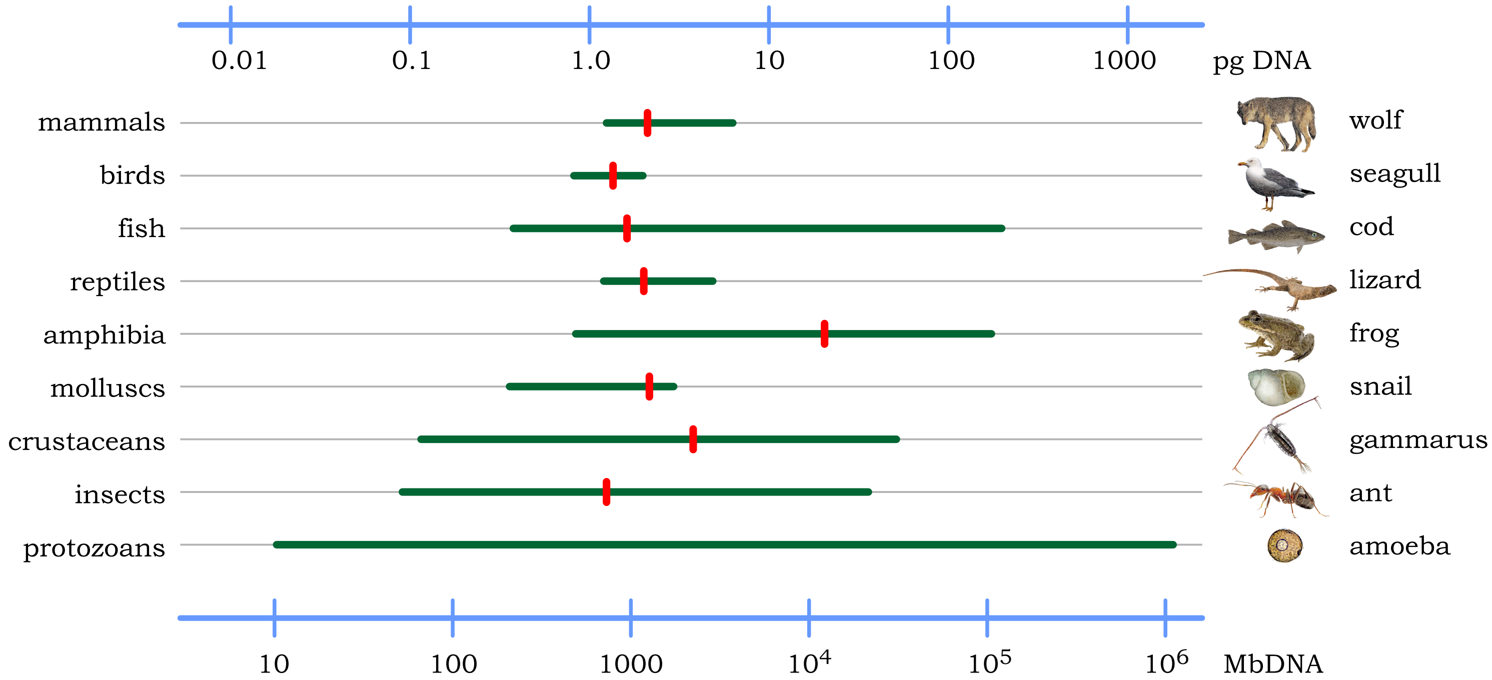


Fig. 11 Genome size shows a tremendous variability across animals, and not in a very obvious manner. The horizontal lines here show the entire span in observed genome size (as pictograms DNA, upper scale, or megabases DNA, lower scale), with the average in red. For certain groups and taxa, there is also a colleration between body size and genome size.

Inside all cells, there are genes, or more correctly the genome, which is the total DNA within a cell. All genes are DNA, but not all DNA are genes. In most organisms, in fact, the majority of the genome is not genes (in humans, less than 2 % of the genome is actually genes. The remaining stuff consists of a variety of DNA of partly unknown functioning. Much of it is virus-like fragments (transposable elements), and the abundance of this can vary in cells, and more of this non-gene DNA can increase cell size. Sometimes we also find duplicated genes or genomes, although this is more common in plants. In homeotherms, there are generally modest variations in genome size, while in fish, amphibians, reptiles and invertebrates it may vary substantially. This has been known for a long time, but is still considered a paradox. The size of the genome do not obey logic rules related to organism size or complexity, there are primitive fishes, even copepods or amobae, that have several times more DNA per cell than we have.

Large cells generally come with large genomes and vice versa, and we still do not know if large genomes demands large cells or if it is the other way around, What is clear, however, it that these basal properties of the inner cells also affects cell size, and in many invertebrates also body size. There are still many unresolved mysteries for future researchers!

The role of oxygen

If we for now constrain ourselves to the marine ecosystem where we find the most striking size spans, with larger organisms typically found in northern or deep waters, what could be the cause for this. We have touched upon temperature, making organisms grow slower, live longer and often attain larger final body size. The direct link from temperature to size for marine invertebrates is not obvious. It could be that although they grow slower, their long life more than compensates for this so they can continue to grow through life. It could however also be that temperature varies along with other drivers – such as oxygen. Warm waters typically have less oxygen, and since oxygen need to diffuse through the cells and be distributed in the body, you may suffer from too little oxygen. In cold waters there is more access to oxygen, which may allow for larger cell- and body size. To this adds also other factors like we have mentioned the role of predators, and also food availability. Northern waters are often more nutrient rich than southern oceans, and more nutrients or food may allow for larger body size.

Larger cells and larger organisms need to be “fuelled” by higher levels of oxygen, and this is also an important part of the earths evolutionary history. For the first 1.5 billion years, the atmosphere on our planet was without oxygen, and it was only after hundreds of millions of years of photosynthesis that oxygen had built up to sufficient levels to sustain higher – and larger – forms of life. Around the “Cambrian explosion” around 550 million years ago, oxygen rose sharply and more advanced life appeared in the sea. It is likely that these two events were connected, that oxygen pawed the way for larger species.

Currently the atmosphere holds 21% oxygen, but in a period of intense photosynthesis 300 milion years ago, oxygen rose towards 35 %, and from this period there are also fossils of gigantic insects, like dragonflies at the size of todays crows and millipeds of 2 meters.

Low temperatures in water means more dissolved gases which could allow for larger animals. This also means that increased temperatures (as we currently see due to global warming) and decreased oxygen in marine waters (which also is a current trend), in fact could promote smaller individuals. Either that larger species are replaced by smaller, or that the species themselves becomes smaller.

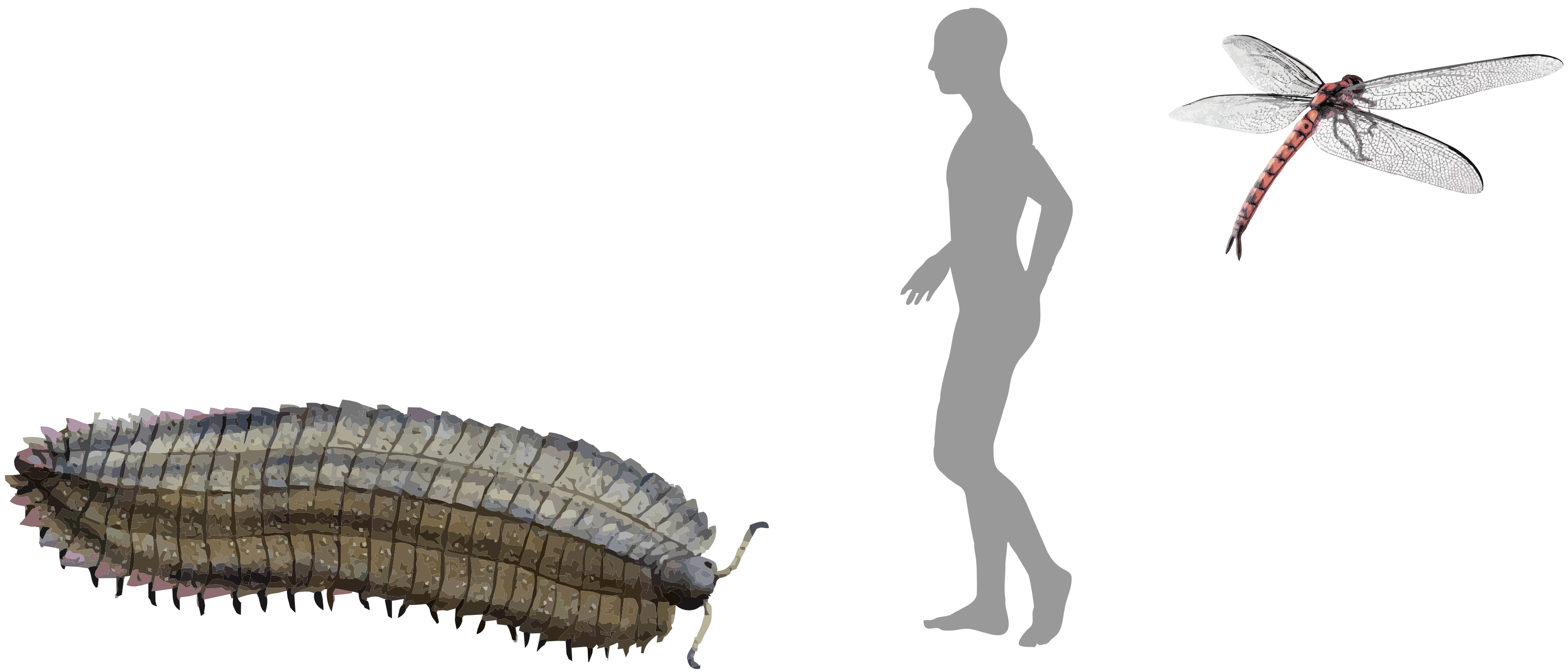


Fig. 12 Examples of giant cambrian invertebrates compared to modern man size. The dragonfly and milipede.

Paleontological records

As the climate changed in the past many times, and the Earth changed from the snow and ice covered snowball in Precambrian epoch to subtropical glasshouse in Mesosoic, the size of organisms responded accordingly. First evidence was the diameter of wormholes left by marine worms living in soft sediment – during the warm Eocene period the holes were of small size – evidently left by small dwellers, while the cooling of the ocean climate in Pliocene resulted in larger organisms leaving wholes of larger diameter.

Sequencing occurrence of large and small species of ancient horses in North America was well correlated with temperature changes – small species prevailed during warm periods and were replaced by larger forms in colder times (Fig. 13).

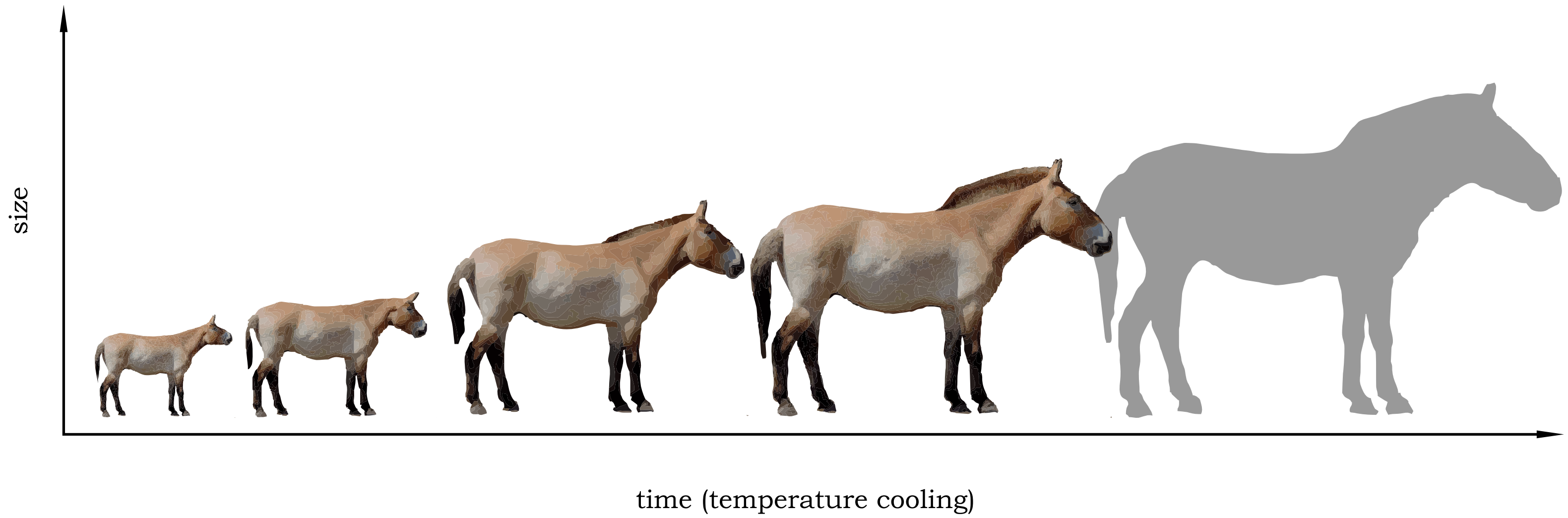


Fig. 13 Like many other mammals horses evolved from small (dog size) forms in warm climate of eocen and as temperatures cooled towards glacial period the size of horse increased to reach in pleistocene the modern form.

Insular dwarfism

Temperature, oxygen, predation (or harvesting) and access to food might all affect size of a given organism or species. Humans that have suffered food or protein shortage generally become smaller which both can be seen geographically and through history. A specific case of dwarfism related to food scarcity are mammals living on small islands. Due to the limited resources and space, they tend to shrink in body size over many generations. Striking examples are the now extinct miniature elephants, hippos and even the hominid species (*Homo florensis*) known from island populations.

Diminishing of body size was discovered even in sauropod dinosaurs, which developed small species on islands during jurasic period. The island shall not be treated literaly – the same effect of genetically controlled diminisment of size can be observed in all isolated populations like those living in osases, lonely mountains and other habitats cut off from the main population exchange.

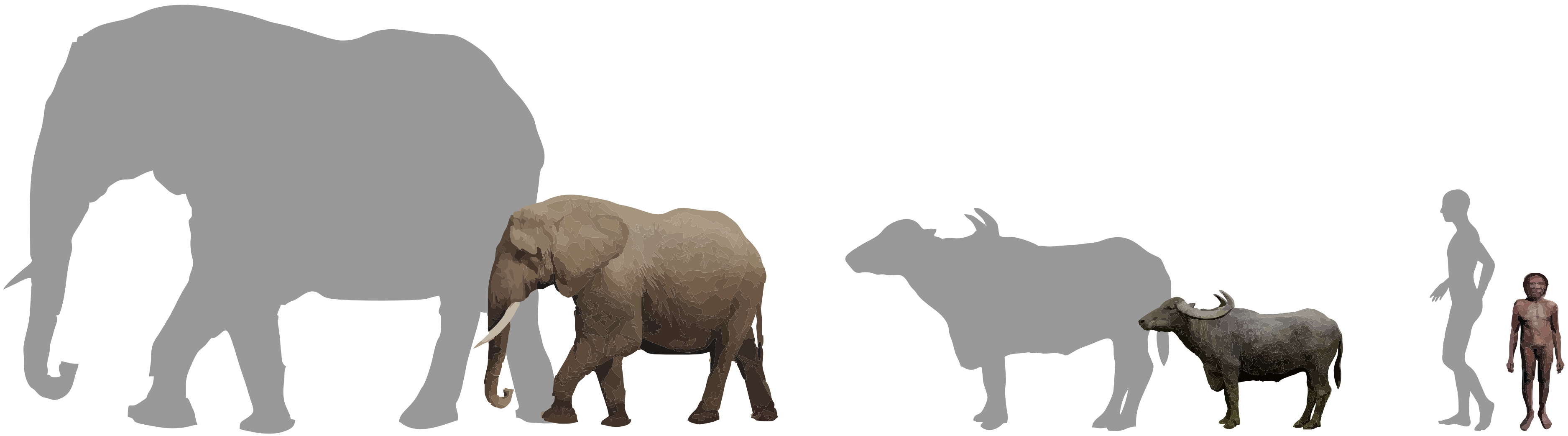
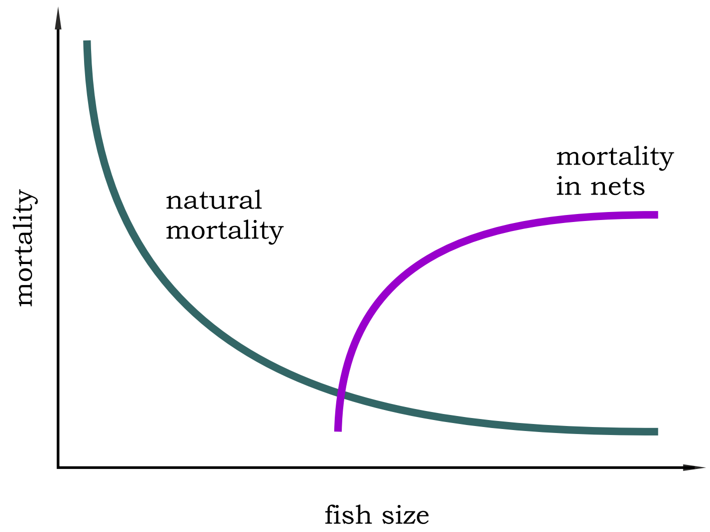


Fig. 14 Insular dwarfism. Bones of small species of elephants, bufflons and hominids were excavated on islands.

Human harvesting affects body size

The management, protection and exploitation of organisms of different size have differed strongly over periods of time with different consequences for body size distribution of populations. For decades, fishermen and hunters were selecting the largest (adult) specimens for the population – to leave the smaller, juvenile individuals to grow and reproduce. Such was the invention of selective gillnet, with mesh size big enough to allow the small fish escape. Removal of largest specimens from the population, that lasted since early modern fishery (beginning of XX century) resulted in decrease of the average size. It turned out, that removing the largest individuals, man removed the animals with the best genes responsible for the large size over time, selecting for smaller individuals. The best survival strategy for commercially fished species was to grow fast and reproduce at small size – thus avoid nets before spawning. This implied over time also a genetic change in the stock, leading to more than 30% reduction of the average adult size. Similarly, hunters have often selected the larger individuals or game with the largest antlers, driving the population towards smaller individuals over time. Here eventually management strategies have shifted, beginning with landowner interested in game animals protecting the largest and most healthy animals, removing the smaller ones- in order to keep the "best genes" in the population (Fig. 15).



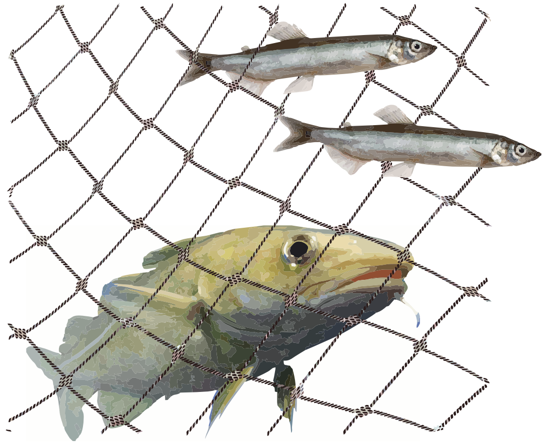


Fig. 15 Fishery pressure effect on the fish size at maturity. Large fish are removed, small are able to escape and spawn.

From an energetic point of view, it may pay off to be small in the sense that given the same resources, a population of smaller individuals may in sum be more productive that a species with larger individuals. It has been recognized long time ago that small animals (e.g. rabbits) compared to large one (cow) will produce biomass much faster from the same amount of food. It is a general rule of bioenergetics, that small organisms are having faster metabolic rates compared to large ones, and consequently complete the life in shorter cycle, and this holds also for marine species (Fig. 16).

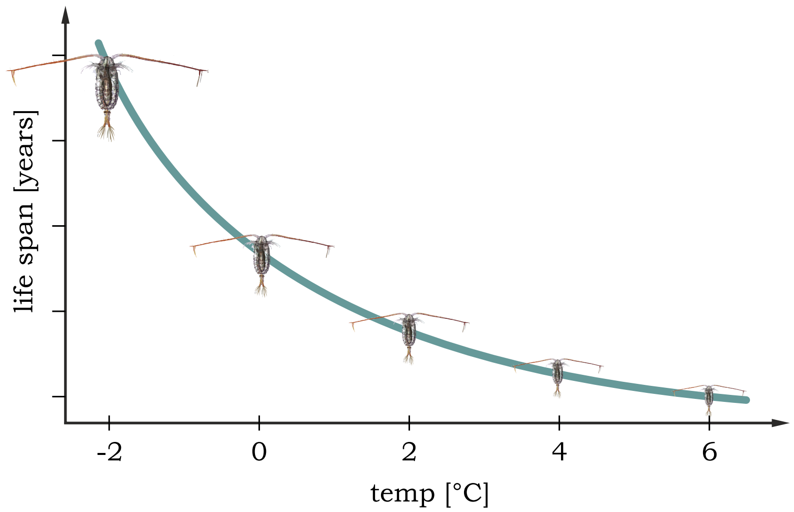


Fig. 16 Size and life span related to ambient temperature.

Food and body size – the Arctic charr case

Among the most striking examples on body size plasticity, and how this is affected by food and life cycle, is the Arctic charr. This species, residing in northern and Arctic lakes commonly split into forms migrating to the sea for some years before returning to freshwater for spawning. Other individuals from the same population decide to stay in the nutrient poor lake. While the migrating animals may reach several kilos after feeding in the ocean, their resident conspecifics will be miniatures reaching only a few grams, despite having the same genotype. Long term data from Sweden show the change in military recruits height from the end of XVIII century to present times – the increase in average height from historical 165 cm to present day 182 cm is related to the improved living standard and better nutrition.

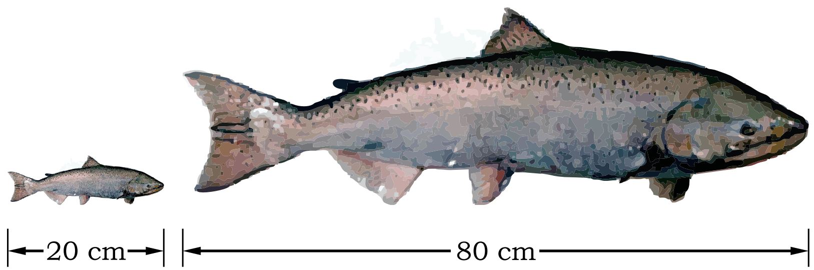


Fig. 17 Dwarf specimen of land locked Arctic charr and the full grown migrating fish of the same age.

Climate effects and future body size

We have seen that temperature and factors related to temperature play a major role in the size of organism, and this may also hold for phytoplankton, perhaps even fish. Since size is important for who eats whom, this also has large implication for ecosystems and food-webs. The ocean is currently warming up at fast pace, and particularly in Arctic waters where we also sea a strong ice retreat. When the surface temperature heats up, there will be less influx of nutrient-rich deep waters, since the warm and shallow upper layers may for an increased resistance towards mixing. This will thus imply reduced nutrients and also reduced oxygen, which may play in concert with increased temperature to promote smaller species.

If such a scenario takes place, the reduced phytoplankton production will mean double-trouble, since less CO_2 will be fixed, meaning that the gigantic drawdown of atmospheric CO_2 that take place today will be reduced, and this is bad news for the climate since more CO_2 will accumulate in the atmosphere and thus give increased warming since CO_2 is a greenhouse gas. The other negative side of this is that there will be less energy at the base of the food web, thus less to eat for the zooplankton which again means less food for fish – and less food for seabirds, seals, whales, polar bears and humans.

Also changed size structure per se will have major impacts, especially if the large, lipid-rich copepods that are keystone species in the marine food web at high latitudes are replaced by smaller, less energy rich species. So far no-one can really tell how far this will go and the full range of consequences, but there is no doubt that changed climate will make a difference here, and that size matters, also in the food-webs.

Suggested further readings

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