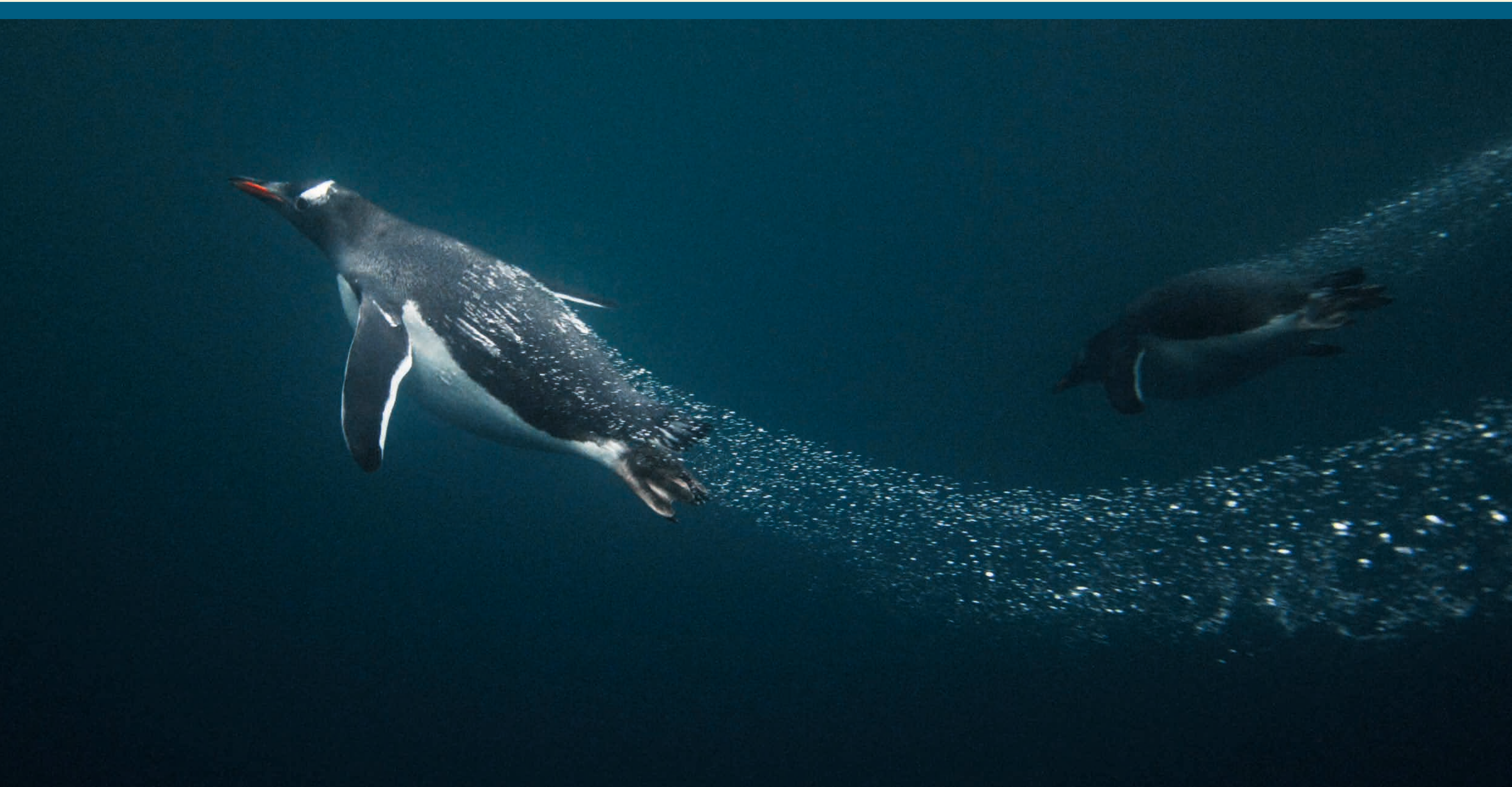
4 Polar flora and fauna

> Short summers, extremely cold winters and vast amounts of ice and snow which reduce the food supply – the Arctic and Antarctic are among the regions most hostile to life on Earth. However, using an impressive range of adaptation strategies, plants and animals have managed to conquer even these areas and have formed globally unique biocoenoses. Yet in times of climate change their future has become highly uncertain.



Living in the cold

> Species diversity in the northern and southern polar regions is primarily determined by geographic conditions. While in the Antarctic almost all life is dependent on the ocean, the Arctic also hosts impressive diversity in its terrestrial areas. Life in both regions flourishes first and foremost during the short summers and subsequently defies the ice and cold by means of remarkable survival strategies.

Three commonalities, many differences

The polar regions' special geographic and climatic conditions present the fauna and flora of the Arctic and Antarctic with particular challenges. For millions of years now, organisms in both regions had to:

- overcome cold to extremely cold ambient temperatures,
- deal with the presence of snow and ice in its various forms, and
- endure extreme seasonal fluctuations of sunlight and temperatures.

The alternating conditions of permanent solar radiation during the polar day and permanent darkness during the polar night mean that plant biomass, and thus food for all higher trophic levels, can only be produced during the summer. During the dark and cold part of the year, those animals which do not migrate to warmer regions must therefore live on their food and fat reserves, consume carrion, or graze on animal and plant residues that have sunk to the sea floor.

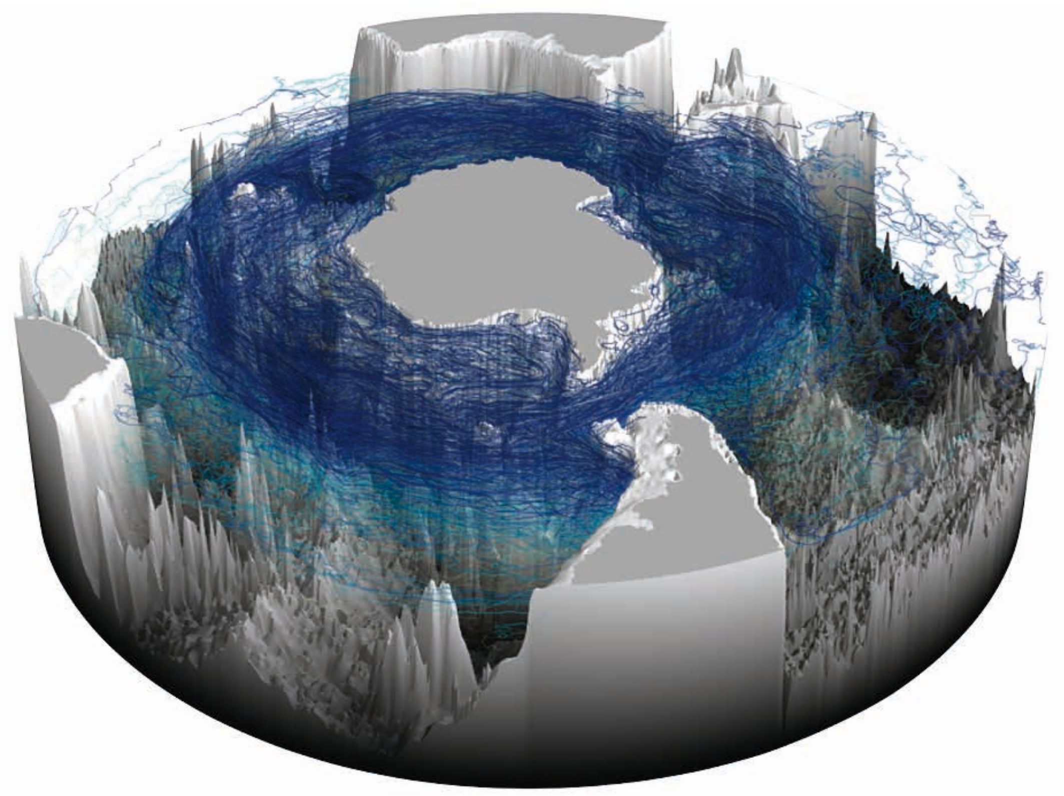
Nonetheless, both the Arctic and Antarctic environments have given rise to a great diversity of life. In the north polar region more than 21,500 species of fauna and flora have now been identified, all of which have adapted to the extreme conditions – from bacteria and viruses living on glaciers and fish that spend the first years of their lives hidden under the marine ice, to the well-known species such as the Arctic fox or the polar bear. There are approximately 14,000 Arctic terrestrial species; a further 7600 species live in the Arctic Ocean.

In contrast, the terrestrial life of Antarctica is relatively species-poor. A mere 1600 animal and plant species occur in the few ice-free terrestrial areas of the Antarctic. The ocean, however, is teeming with life – some 10,630 species have been identified, with the majority displaying special adaptation mechanisms that can be found nowhere else on Earth.

A matter of geographic location

A comparison of the ecosystems of the two polar regions highlights the significant differences between them. While there are large-scale, glacier-free areas of tundra and extensive river systems in the Arctic, both of which produce sufficient biomass during the summer to feed even large herbivore species such as caribou and musk oxen, 98 per cent of the Antarctic landmass is still covered in ice. This means that lichens, mosses and higher plants can hardly find substrates on which to grow. Therefore, the main food source for all the animals native to the Antarctic is the ocean which completely surrounds the continent.

The resultant isolation of the Antarctic from the rest of the world has had a similarly lasting impact on the development of life in the south polar region as its glacial history. For more than 34 million years now, oceanic basins more than 3000 metres in depth have separated Antarctica from the surrounding land masses of South America, Africa and Australia. Even at its narrowest point, at the Drake Passage, the Southern Ocean is still 810 kilometres wide. Terrestrial species of fauna intent on migrating to Antarctica from temperate latitudes would have had to be capable of long-distance flights or swims even in the past. Once they had overcome that obstacle, the Antarctic immediately presented them with the next challenge – several times over the past millions of years the southern continent became completely covered in ice, sometimes even beyond its coastline. The Antarctic terrestrial species were left with the choice to either migrate or to move out onto the marine ice. Otherwise they faced extinction.



4.1 > A three-dimensional model of the Southern Ocean. With its deep basins and circulating water masses, it continues to form a barrier that many animal and plant species from more northern latitudes can scarcely overcome. Similarly, it has prevented species native to the Antarctic shelf sea areas from migrating northwards.

In comparison, settling in the Arctic was much easier as it is directly connected to large continental land masses stretching far south and into warmer climatic zones. Eurasian and North American species of fauna and flora adapted to the cold were therefore able to colonize the north polar region by land. When during the last glaciation large ice shields formed in the Arctic, this did not generally spell the end of terrestrial life in the way it did in Antarctica. For one thing, the Arctic species had the opportunity to shift their ranges toward the south and thus to flee from the ice. Moreover, during this glaciation the Arctic was never entirely covered by glaciers and ice shields. Regions such as Beringia and eastern Siberia remained ice-free and served as a refuge for many organisms. As a result, the north-eastern tundra regions of Russia are among the most species-rich terrestrial areas of the Arctic to this day.

Given that the Arctic is not separated from more southern climes by oceans or high mountain ranges it is not surprising that the north polar region hosts many terrestrial predators such as polar bears, wolves and Arctic foxes while there is not a single four-legged predator species in mainland Antarctica. Instead, millions of penguins breed in the Antarctic – birds that cannot fly and that know no enemies outside of oceanic waters. If penguins were resettled in the Arctic, they would easily be picked off by polar bears and other predators, given that these large birds have no intuitive sense of danger when on land. The only bird species resembling penguins which ever lived in the Arctic was the flightless great auk *(Pinguinus impennis)*. It lived on remote rocky islands in the North Atlantic were there were no polar bears, wolves or foxes. However, in the early 19th century European seafarers discovered the birds' colonies. They hunted the defenceless auks to extinction in a mere four decades. The last great auks were killed in June 1844 on the Icelandic island of Eldey.

4.2 > Four endemic species of true seals are at home on and underneath the jagged Antarctic pack ice. These include the crabeater seal, Ross seal, Weddell seal and leopard seal.

A "biodiversity pump"

The geographic conditions in the Arctic and Antarctic have also had a decisive impact on the species diversity of the polar seas. The ring-shaped Southern Ocean made it possible for many of its inhabitants to establish ranges encircling the entire continent. At the same time, the Circumpolar Current, which reaches great depths, and the rapidly decreasing water temperatures at the top 200 metres of its water column impede the migration of species from more northern climes. Moreover, water temperatures have decreased since the Drake Passage opened 34 million years ago – at first there was only episodic cooling and interim warming phases but in the past 15 million years temperatures have continuously declined. The Southern Ocean is on average ten to twelve degrees Celsius colder today than it was 40 million years ago.

Sea ice conditions in the Antarctic changed in step with the cooling of the Southern Ocean, with far-reaching consequences for life in and underneath the sea ice, in the water column, and on the sea floor. The more ice formed in the Antarctic in the course of a cold period and the further glacial and shelf ice masses expanded out into the ocean, the less space there was for residents of the shelf, such as sea-floor dwelling sponges or starfish. Many shallow-water areas became completely uninhabitable and formerly conjoined marine regions were separated by the glacial advance. Scientists believe that many of the marine organisms inhabiting the continental shelf seas at that time were forced to migrate down the continental slope or into the deep sea. At the same time, however, the current assumption is that the isolation of habitats of the continental shelf gave rise to new species. Since the Antarctic ice masses have repeatedly expanded and contracted over the past 2.1 million years, biologists speak of a "biodiversity pump". The premise here is that the repeated isolation of biocoenoses (cold period, growth of ice mass) and the subsequent opportunity for expansion (warm periods, retreating ice) provides perfect conditions for the evolution of a unique and highly differentiated species diversity which, moreover, includes a high proportion of endemic species, i.e. species of fauna and flora that can only be found in the Antarctic. Approximately 50 per cent of Antarctic sea squirts, anemones, bryozoans, mussels and sea spiders are endemic species; roughly 75 per cent of sea snail species are endemics and for Gammaridea, a suborder of amphipods, as well as for octopuses the proportion of endemic species is as high as 80 per cent. In this way the Southern Ocean has given rise to a much greater and more colourful level of biodiversity than one would expect at first sight. Biologists have identified more than 8000 different species of invertebrates in the Antarctic, and some regions have not even been properly studied as yet.

The fish fauna of the Antarctic continental shelf seas is dominated by a group of Antarctic fish termed Notothenioidei. They constitute more than 70 per cent of species diversity and more than 90 per cent of fish biomass in the continental shelf seas. However, there are also faunal groups for which to date there are only occasional sightings in the Antarctic continental shelf seas, the red king crab for example, or which as yet do not occur in the Antarctic. The latter include lobster and hermit crabs, which also explains why the benthic fauna of the continental shelf has not developed defence mechanisms against clawed predators.

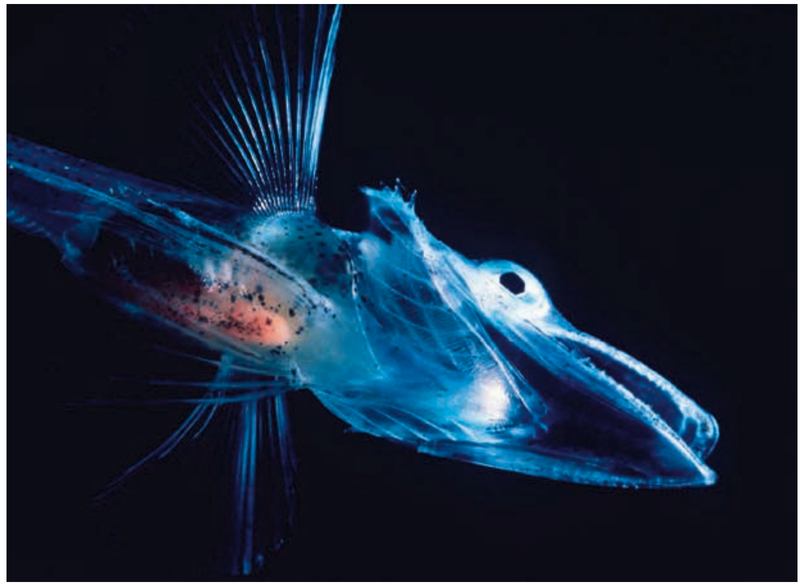
Southward migration

Geologically speaking the Arctic Ocean is younger than the Southern Ocean which means that species of high northern latitudes had less time to adapt to polar conditions than the southern fauna. But they, too, had to survive periods of large-scale ice formation, for example some 140,000 years ago when major ice shields covered North America and northern Europe and pushed their up to 1000 metres thick shelf ice onto the entire Arctic Ocean, which presumably became completely frozen over.

At that time, the biocoenoses of the Arctic Ocean either withdrew to greater depths or they migrated to more southern latitudes along the Atlantic and Pacific coastlines. When the ice masses slowly disappeared it took some time for the marine organisms to recolonize the Arctic ecosystems. Biologists therefore consider the diverse biocoenoses of the Arctic marginal seas to be not much older than 125,000 years. Moreover, in the Arctic Ocean scientists distinguish between the Atlantic and the Pacific sector respectively. Their inhabitants migrated from the respective neighbouring ocean and separately adapted to the polar conditions. It is for this reason that to this day different species play the exact same role in the two sectors' ecosystems.

In the Arctic, furthermore, it has been and still is much easier than in the Antarctic for inhabitants of the continental shelf seas to migrate from one continent to the next, given that the northern coastal areas of Europe, Asia and North America share contiguous offshore shelf areas. Antarctica, in contrast, lacks such a shallow water connection to neighbouring continents. In the Antarctic, therefore, the pressure to adapt has always been much higher than in the Arctic. During cold periods, marine organisms of the Southern Ocean had significantly fewer refuges at their disposal than species of the far north. The organisms of the Southern Ocean had only two options – they either adapted or they became extinct. It is for this reason that Antarctic marine life developed significantly more sophisticated adaptation mechanisms than the inhabitants of the Arctic Ocean.

4.3 > Antarctic white-blooded fish such as this juvenile blackfin icefish inhabit the world's coldest marine regions and have no haemoglobin in their blood.



4.4 > In order to escape the Arctic winter cold, the Arctic tern *(Sterna paradisaea)* leaves its Arctic breeding areas in August and flies to the edge of the Antarctic pack ice zone. In the course of this migration the birds cover a distance of some 35,000 kilometres – the greatest distance covered by any migratory bird species.

Survival tactics of terrestrial animals in the polar regions

Conditions in the Arctic and Antarctic are characterized by extreme fluctuations over the seasons. In summer there is sunlight, warmth, ice-free terrestrial and water surfaces and an overabundance of food resources; in winter, however, conditions are the exact opposite. In the Arctic, for example, winter surface temperatures drop to around minus 40 degrees Celsius for weeks, and minimum temperatures of minus 50 to minus 60 degrees Celsius are not uncommon. There are also major temperature differences between north and south as well as between coastal regions and more inland areas respectively. Such contrasts can only be survived by species that adopt one or more of the following survival tactics:

- fleeing the cold by migrating to warmer areas (migration),
- surviving the winter in a protected location (dormancy or hibernation),
- optimizing body heat regulation, and
- provisioning by means of accumulating large body fat reserves.

Fleeing from hunger and cold

The flight from low temperatures and food scarcity is a tactic used primarily by the many seabirds occurring in the polar regions. The Arctic hosts a total of 200 bird species, the majority of which are geese, ducks, shorebirds and seabirds. Compared to temperate regions there are few songbirds. Most of the Arctic bird species spend only a few summer months in the far north. As winter approaches, 93 per cent of the species migrate to warmer regions. Their migration routes lead to regions all around the world. While many of the geese, passerines, owls, birds of prey, auks and gulls overwinter in adjacent temperate latitudes, some of the shorebirds, phalaropes, and the Sabine's gull *(Xema sabini)* migrate as far as to the tropics and Australia. The bar-tailed godwit *(Limosa lapponica)*, for example, flies 12,000 kilometres from its breeding area in Alaska over the Pacific to New Zealand. Long-distance migrants such as the Arctic tern and skuas even target Antarctica where they overwinter on the edge of the Antarctic pack ice zone. This means that on their way from the Arctic breeding areas to the Antarctic overwintering areas and back the birds cover a distance of up to 80,000 kilometres per year. But this effort is worth it as both polar regions provide the birds with an abundance of food during the summer. And as the Arctic terns rely primarily on their eyesight for hunting they benefit significantly from the fact that in their chosen habitats the sun does not set for a total of eight months, enabling them to theoretically hunt for prey around-the-clock.

However, there are also bird species in the Arctic that do not migrate to warmer areas. Among the terrestrial birds, these include the common raven *(Corvus corax)*, rock ptarmigan *(Lagopus muta)*, snowy owl *(Bubo scandiaca)* and Arctic redpoll *(Acanthis hornemanni)*. Among the

4.5 > A herd of caribou moves through the Arctic National Wildlife Refuge in October in search of food. At this time the region has already seen snowfall which means that the animals need to scrape away the snow from potential grazing areas.

seabirds that spend winter in the far north are the black guillemot *(Cepphus grylle)*, thick-billed murre *(Uria lomvia)*, ivory gull *(Pagophila eburnea)*, Ross's gull *(Rhodostethia rosea)* and common eider *(Somateria mollissima)*.

Mammals also undertake seasonal migrations – baleen whales for example or reindeer *(Rangifer tarandus)*, known as caribou in North America. In eastern Alaska as well as in the Canadian Yukon Territory, for example, every spring a herd of between 100,000 and 200,000 of the so-called Porcupine caribou undertakes a 1300 kilometre northward migration to the coastal plains of the Arctic National Wildlife Refuge where the females give birth to their calves. The kindergarten on the coast of the Arctic Ocean offers many benefits to the wild herd. The landscape is flat and without forest cover, allowing the caribou to spot potential predators such as bears or wolves from afar. The fresh ocean breeze keeps the annoying mosquitoes in check, and there is a plentiful supply of food and water. At the end of the summer the caribou start on the return journey to their winter territories in the more southern Ogilvie Mountains. Other herds migrate even further south and overwinter in the subarctic boreal forests. But a few herds spend the winter in the tundra.

Homoeothermic or poikilothermic

Birds and mammals have a unique characteristic in the animal world: They are the only organisms able to maintain a constant internal body temperature regardless of external temperatures, which is why they are called homoeothermic or endothermic organisms. The internal body is taken to include those areas of the torso and head containing all the vital internal organs (intestines, central nervous system, and brain) that also generate heat when the organism is at rest. The body core temperature is generally more or less constant while the temperature of the body shell, including the skin and extremities, fluctuates more strongly.

The body core temperature of humans is 37 degrees Celsius. Hedgehogs have a core temperature of 35 degrees Celsius and swallows of 44 degrees Celsius. The body core temperature of carnivores, horses and humans fluctuates by one to two degrees Celsius throughout the day dependent on activity. An increase of more than six degrees Celsius is life-threatening to most homoeothermic organisms and generally results in death by hyperthermia. In contrast, death by hypothermia occurs when an organism's body temperature decreases and its body core temperature falls below a species-specific level. Humans for example are in a critical condition if the temperature of their blood falls below 27 degrees Celsius.

Fish, amphibians or reptiles are not greatly impacted by a slight drop in body temperature. They are among the poikilothermic organisms or ectotherms. These terms are used for all organisms whose body temperature is fully dependent on the temperature of their environment and is generally not influenced by the animals' metabolism. Poikilothermic animals have developed characteristic behaviours which allow them to regulate their own body temperature. Salamanders for example bask in the morning sunshine in order to reach "operational temperature" while many flying insects warm up by means of rapid contractions of their wing muscles.

Thermoregulation

Just like all other homoeothermic animals in the polar regions, these caribou face the challenge of maintaining their body core temperature at a level of between 37 and 41 degrees Celsius despite the air around them being up to 100 degrees Celsius colder. The only way to achieve this is to prevent the loss of body heat to the environment. This is a difficult task as body heat can be lost in three different ways:

- by heat conduction,
- by heat radiation and
- by evaporation.

The animals must control all three processes to conserve body heat. Homoeothermic species have developed a range of remarkable behaviours in order to minimize heat loss. Among others, these include:

- curling up into a ball (reducing the body surface to volume ratio),
- huddling together in a group for mutual warmth,
- withdrawing to a protected location,
- accumulating a warming layer of fat or a double layer winter coat or plumage, and
- cooling down their breath and extremities.

4.6 > Polar bears are very good swimmers and, as this large male demonstrates, they are also good divers. However, the animals get cold very quickly in the water. On long-distance swims mature bears with a thick layer of body fat for insulation have better chances of survival than juvenile bears.

To curl up means to make yourself as small as possible. Many species, from polar bears to Arctic redpoll, curl up into a ball in winter or draw in their head and limbs so as to minimize their body surface. The more spherical the body, the smaller is its surface to volume ratio and the less heat is lost by the animal by way of conduction or radiation. Polar bears often cross their paws over their muzzle as they lose most body heat from their nose and face which is covered in only sparse hair.

Animals living in groups, herds or colonies often stand closely together in order to warm each other and thus to minimize their own heat loss. The most well-known example is the circular "huddles" of emperor penguins in Antarctica. In winter when ambient air temperatures can be as low as minus 50 degrees Celsius and the males must stay on the ice to incubate the eggs, the birds huddle together by the thousands and so closely together that up to ten penguins may be squeezed up on a square metre of ground – back to belly, side-by-side and with the head placed onto the shoulder of the penguin in front. In the middle of this giant incubator the air warms to up to 24 degrees Celsius. This is however too warm for the birds at the centre who gradually seek to escape the heat. The birds on the margins meanwhile are cold and slowly push towards the centre. This is why the penguins continuously change their position and why the huddle is constantly moving with each bird at some point enjoying the warmth. In this manner these large birds are able to reduce their heat loss by half even during the harshest of winter storms. Arctic musk oxen display similar behaviour. On cold days the members of the herd form a tight circle, allowing the animals to warm each other and collectively remain relatively unimpacted by icy winds.

A third strategy employed to reduce heat loss is to withdraw to a protected area. This could be a cave or else the animals may curl up and let themselves get snowed in. Polar bears, wolves, foxes, hares and ptarmigans are known to at least temporarily seek shelter in snow dens during the winter. Smaller Arctic species such as lemmings or stoats must even spend most of the winter underneath the insulating snow cover due to their small size and the associated heat loss. Dependent on the thickness of the snow cover, temperatures may be as high as zero degrees Celsius, allowing these small mammals to survive.

Birds and mammals overwintering in the polar regions also protect themselves from the freezing cold by means of a dense winter coat or plumage. In mammals and birds which need to enter the water in search of food, or in whales which spend their entire lives in the ocean, a thick layer of fat (blubber) generally takes on this insulating function. Just how well feathers or fur can conserve body heat depends on two factors, one being the individual thermal conductivity of each individual hair or feather, the other being the degree to which the coat or plumage is able to trap an insulating layer of air near to the body, as the thermal conductivity of air is only half that of hairs or feathers. Presumably this is the reason why the guard hairs of caribou are hollow and internally sectioned into thousands of tiny air cells, each separated from the next by a thin wall. In this manner, the animals' guard hair does not only protect them from external influences such as snow or rain, it also forms a second and very effective layer of insulation in addition to the underfur.

The fur's insulating characteristics differ significantly between species, with the ability to retain heat generally increasing with the thickness of the layer of fur. The insulating effect of the fur or plumage can be further increased by fluffing up the plumage or erecting the hairs, thus trapping a greater amount of insulating air near to the body. Small furry mammals such as lemmings or stoats are clearly at a disadvantage when it comes to keeping themselves warm by means of their body hair. They need a short-haired coat that still allows them to move.

But the large mammals with rather thick coats must also pay attention to a number of factors so as to avoid dying of hypothermia. The polar bears' long guard hair for example provides superb insulation as long as the coat is dry. However, when the bear jumps into the sea, for example in order to swim from one ice floe to the next, water reaches the skin, and water conducts heat away from the body 25 times faster than air. At moments like that fully grown bears trust the insulation provided by their thick blubber which reaches a thickness of up to 11.4 centimetres. For bear cubs, however, a swim like that can be very dangerous as they lose heat very rapidly. They are similarly at risk when it rains as both rain and sleet considerably impair the functional characteristics of fur or plumage.

Icy winds can also result in significant heat loss. When wind passes through fur or plumage it swirls the layer of air close to the body, thus reducing its insulating function. Snowy owls, for example, that are exposed to 27 kilometre per hour winds at an ambient temperature of minus 30 degrees Celsius lose heat so quickly that in order to not freeze to death they need to generate twice as much heat as would be required if the air was still. In contrast, the guard hair and underfur of reindeer and musk oxen provides such complete insulation that the animals loose little or no heat even during winter storms.

Whales, polar bears and seals protect themselves from the cold by means of thick blubber. While the insulating capacity of this layer of fat is not as great as that of fur, it is also functional in the water where fur generally fails as a means of protection. This layer of fat can be impressively thick. In bowhead whales *(Balaena mysticetus)* it can reach a thickness of up to 30 centimetres. And just like the coats of reindeer and musk oxen, blubber also changes with the seasons, at least in seals. Their blubber is at its thinnest in summer when the animals' moult forces them to stay on land and fast. In the run-up to winter they fatten up again and blubber thickness increases.

Penguins such as Adélie and emperor penguins protect themselves from the icy cold by means of a plumage that offers superb insulation. However, when they are diving in the sea the feathers are compressed and the trapped air is expelled which means that the plumage loses its insulating properties. The birds' blubber then protects them to some extent from heat loss.

The queen of the tundra

The Arctic bumblebee species *Bombus polaris* is one of the first insects to be seen flying in the tundra in springtime. *Bombus polaris* differs from most other insects in that it is not greatly impacted by cold spring air. Even though as an insect it is an ectothermic organism, this bumblebee has found ways to stay warm. On sunny days the queen and her workers sit exposed to the sun for a while in order to warm up their bodies. The quickest way to do that is to bask inside an Arctic poppy flower *(Papaver radicatum)*. The petals of its conical flower act like mini-mirrors, reflecting sunlight into the centre of the flower.

When cloud cover impedes sunlight the bumblebees turn on their internal heating system – they begin to shiver their large flight muscles which allows them to bring their body temperature up to the minimum flight temperature of 30 degrees Celsius even if the ambient temperature is significantly lower. The Arctic bumblebee's thick coat of hair helps them to trap and conserve this heat.

Their ability to utilize thermoregulation allows the Arctic bumblebees to start foraging for food as early as May, at a time of spring when the cold still forces most other insects in the Arctic into a state of torpor. And this bumblebee is in a hurry – the queen's first task as the only member of its colony to survive the winter is to gather pollen and nectar in order to gain strength. Next she will build a nest in a subterranean burrow and produce an initial brood consisting only of workers as the foundation of a new colony. In late summer the queen lays eggs for a second time. This brood produces drones (males) and hundreds of queens. However, on average only one queen per colony survives the coming winter. The old queen dies along with the other members of its colony.

Bombus polaris occurs in the northern tundra regions of Alaska, Canada, Scandinavia and Russia and is considered a key pollinator in these regions. There is only one other bumblebee species, *Bombus hyperboreus*, that survives this far north of the polar circle. In cuckoo-like fashion its queens like to enter and take over Arctic bumblebee nests. They deposit their eggs and let *Bombus polaris* workers take care of the brood.

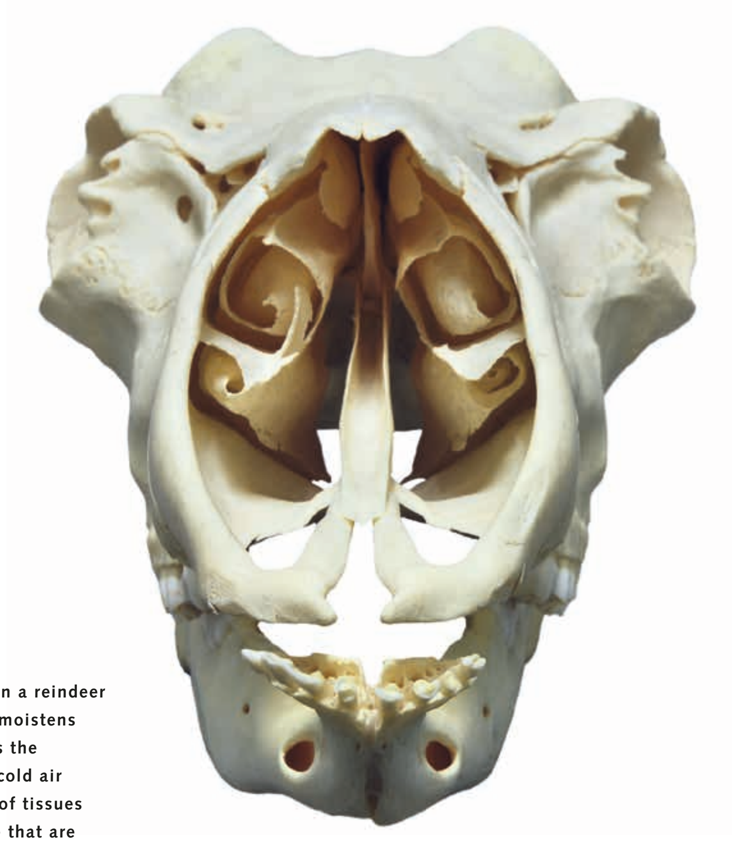
4.7 > The Arctic bumblebee species *Bombus polaris* flies even in cold weather. The inspect generates the body temperature needed for this by basking in the sun or by shivering its flight muscles.

Physiological protective mechanisms against heat loss

Animals can also prevent the loss of body heat by conduction if they cool down external body parts or their limbs while maintaining a constant body core temperature. This type of behaviour is displayed by, for example, reindeer, emperor penguins and gulls. Under certain circumstances they are able to lower the temperature of their feet to close to freezing while their body core temperature remains at a normal level.

The often badly insulated extremities can be cooled down to this extent as the blood vessels in legs, wings or flippers are located so closely together that heat can be exchanged between arteries and veins. Warm arterial blood originating in the centre of the body passes on its heat to venous blood which had previously cooled down in feet or fins and is being transported back towards the body core.

In this way, only blood already cooled down reaches the extremities, thus greatly reducing heat loss from feet, flippers or wings.



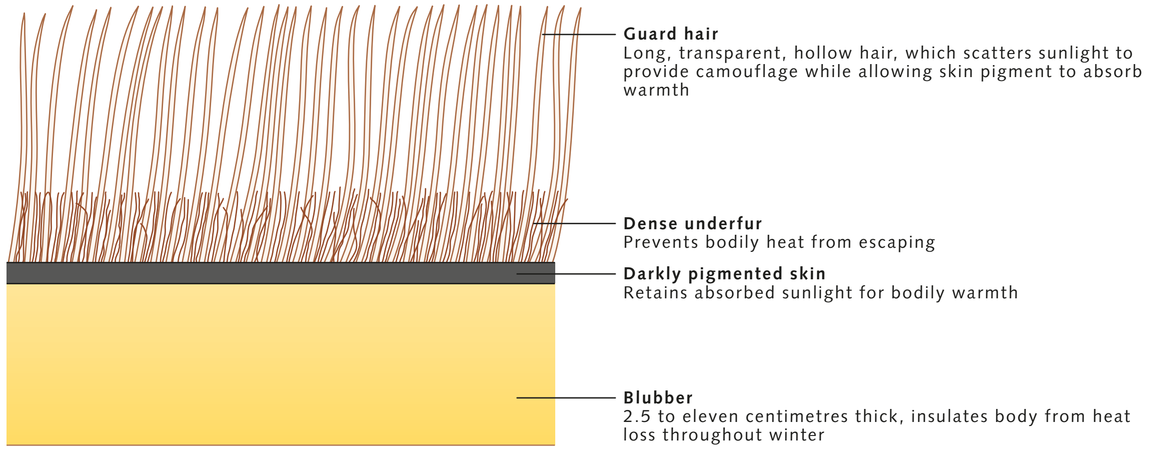
4.8 > When a reindeer inhales it moistens and warms the incoming cold air by means of tissues in its nose that are richly supplied with blood vessels. These tissues are supported by curled, thin bone structures, clearly visible in this photo of a reindeer skull.

Reindeer have such long legs that the close proximity of veins and arteries alone is sufficient for heat exchange. In the seals' short flippers, however, the heat exchange is amplified by the veins branching into blood vessels surrounding the centrally located artery which conducts heat to the veins. Moreover, the animals can regulate their blood flow and thus also the heat supply to their extremities – they may want to reduce heat loss in a cold environment, or they may want to quickly cool down, for example following major exertion or when they are at risk of overheating.

Surprisingly, the animals do not lose sensation in their wings, flippers or paws even when these have become very cold. Impulse transmission in nerves and muscles of the ball of the foot of Arctic wolves and foxes continues to function even when the animals stand on cold surfaces with temperatures down to minus 50 degrees Celsius and their paws have cooled down to freezing point. Studies have shown that the muscles and nerves in poorly insulated extremities still function when the tissue has reached a minimum temperature of minus six degrees Celsius – an adaptive mechanism that appears to be widespread among mammals and birds in high and medium latitudes.

A similarly sophisticated system helps animals to not unnecessarily lose heat and water vapour to the environment when breathing. When a human exhales at an ambient temperature of minus 30 degrees Celsius, one can see the roughly 32 degree Celsius warm and moist breath as it exits the nose in the form of a light cloud of vapour. Reindeer, in contrast, do not produce such a cloud. The air they exhale is dry and cooled down to 21 degrees Celsius, thus reducing water and heat loss to a minimum. Once again, the secret of these energy savings is effective heat exchange which in this case happens in the nose. In contrast to the human nose, the nasal cavity of reindeer contains numerous convoluted muscous and other membranes that are richly supplied with blood. This nasal structure is highly beneficial in two ways: Firstly it increases the surface area of muscous membranes along which inhaled or exhaled air passes. This gives the reindeer sufficient opportunity to expel or retain heat and water in its breath. Secondly, the complex nasal anatomy divides the breath into numerous thin layers of air, thus further optimizing heat exchange.

When a reindeer inhales, the icy cold polar air passes over the well-perfused nasal membranes. In less than a second it is moistened and its temperature is raised to the animal's body temperature. The air reaching the lungs has a temperature of 38 degrees Celsius and is sufficiently moist to ensure optimum oxygen uptake. As a result of the heat transfer to the inhaled air, the membranes briefly cool down. When the animal exhales, its warm breath once again passes the now cooled nasal membranes and transfers back some of the heat. This cools down the breath to 21 degree Celsius and most of the water vapour it contains condenses. This mechanism ensures that reindeer exhale only cool and dry air, thus saving a great deal of body heat and moisture. The latter is critical in particular when all ponds, rivers and lakes are frozen during the winter and the animals are forced to consume snow in order to obtain water.



4.9 > A thick layer of blubber and warming underfur protects polar bears from losing body heat to their environment. Moreover, the transparent guard hairs allow for solar radiation to reach the skin which means that the bears can warm up in good sunny weather.

Despite their thick winter coat and their sophisticated heat-conserving mechanisms it is possible for the animals to lose heat and for their body temperature to drop to dangerous levels. When this happens, most of the animals increase their metabolism and begin to shiver, generating heat by means of muscle contractions. Wind and moisture generally accelerate heat loss while sunshine can help the animals to maintain their body temperature. Harp seals, for example, bask in the sun when they are cold, a strategy also employed by polar bears. Their long transparent guard hair is particularly suited to letting solar radiation pass through, allowing for its optimum absorption by the bears' black skin.

The polar bears' guard hair also has another special characteristic. It absorbs the longwave heat radiated by the bears themselves. Simply put, it re-absorbs much of the heat radiated by the bears despite their thick underfur. This means that the animals lose very little heat from their body surface. However, this can also be disadvantageous, for example when the bears move swiftly. It can quickly put them at risk of overheating. This is the reason why most of the time polar bears move at a rather leisurely pace. And if they ever get too hot after all, these largest of all terrestrial Arctic predators cool down by jumping into the water.

That option is not generally available to reindeer, even though they often overheat especially in winter under conditions of great exertion. At such moments, reindeer cool down the most critical parts of their brain by directing cold blood from their nasal membranes through a facial vein towards their brain. Just before reaching the brain, a heat exchange takes place with the blood flowing through the carotid artery. This mechanism ensures that only blood at normal temperature circulates in the brain while the surplus heat is distributed to the rest of the body until such time as the strain has subsided and the heat can once again be exchanged by the nasal membranes.

Thermoregulation in young animals

In the polar regions, animal offspring is born at very different times and under a variety of conditions. Nonetheless, all young animals have one thing in common – their ratio of body surface to body mass is significantly worse than that of their parents, which means that young animals suffer relatively greater heat loss. Most of them are born without fur or plumage, or if they are, then its insulating powers are not nearly as good as their parents' coat. This is a particularly perilous situation if the young birds or mammals are wet at birth.

Polar birds and mammals have developed special behaviours to ensure that their offspring have a chance at survival. Altricial species the young of which require a lot of parental support at the start, such as polar bears or lemmings, generally give birth at a protected location, such as

4.10 > As can clearly be seen in this infrared image, polar bears primarily lose body heat from their noses which are only sparsely covered in fur.

a snow cave, den or nest. While a polar bear female is forced to fast for the first three months after giving birth because she never lets her cubs out of her sight, lemming females must leave their young at times in search of food while their pups stay behind in the burrow on their own. During this period the baby lemmings' body temperature drops to well below 20 degrees Celsius but this does not kill them. During the first days of their lives they are surprisingly immune to cold. The older the pups are, the better they get at regulating their own body temperature. The strategies they employ include muscular heat generation (shivering), a thicker fur, or the burning of fatty acids from their brown fat, a process often described in the special literature as nonshivering or biochemical thermogenesis.

Brown fatty tissue can be found in almost all newborn mammals. Its cells are significantly smaller than those of the white, insulating fatty tissue. It contains many small lipid droplets and a particularly large number of mitochondria, the cells' power plants. The breakdown of lipids in mitochondria generates heat which enables a variety of polar mammal species to survive.

In contrast, newly hatched birds are dependent on being kept warm by their parents. Antarctic procellariids (a group of seabirds including petrels and shearwaters), for example, hatch at an average temperature of minus 25 degrees Celsius on bare rock. Once the chicks are hatched, their parents must keep them warm for at least eleven days. The chicks of emperor penguins hide in their parents' brood pouch for up to 50 days – initially that of the male, and subsequently in the female's brood pouch when she returns from the ocean and for the first time feeds the chick food sourced at sea.

Reindeer calves and ptarmigan chicks must stand on their own feet from day one. They are precocial species. Unlike penguin chicks they are born with their own protection against the cold. Ptarmigan chicks hatch with warming plumage, are strong enough to walk long distances even on their first day, and are able to maintain their body temperature by means of breast muscle shivering. Nonetheless, the little ptarmigans seek their mother's warmth when their body temperature drops to below 35 degrees Celsius. Young reindeer and musk oxen get cold in particular when there is wind, rain or sleet. At such times their coat loses its warming traits much faster than that of their parents. The offspring primarily resorts to the burning of lipids from their brown fatty tissue in order to stay warm. Most seal pups in the polar regions must also avoid the water. They are born with a woolly and normally white covering of lanugo which only keeps them warm as long as it stays dry.

Body heat generation requires energy which the offspring of mammals obtain from their mothers' milk. The milk of species that are at home in the polar regions is particularly high in fats. In whales, seals and other marine mammals the milk's fat content is between 40 and 50 per cent, while the milk of terrestrial species contains between ten and 20 per cent fat. (For comparison: normal cows' milk has a fat content of roughly four per cent.) The young of different species are suckled for different lengths of time. While hooded seals nurse their pups for only two to four days, walrus calves suckle for more than a year.

When food becomes scarce

Animals in the polar regions must not only deal with extreme air and water temperatures. They are also faced with the challenge that they can only find sufficient amounts of food at certain times of the year. Different species solve this problem in very different ways. Musk oxen, for example, can lower their metabolism by 30 per cent. Similar observations have been made in Arctic foxes, Arctic hares and ptarmigans. The animals also limit their movement radius in order to save energy. Reindeer on Spitsbergen spend up to 80 per cent of the day in a standing or lying position during the winter as any amount of exertion and any additional step in the snowy terrain has a price. If the animals begin to trot their energy consumption quadruples even if the herd moves at only a moderate pace of seven kilometres per hour.

For this reason, most of the animals build up major fat reserves in times of plenty as something of an "insurance policy". As early as in August, ptarmigans on Spitsbergen begin to eat anything and everything they can find. By November the birds will have gained so much weight that their layer of fat comprises 30 per cent of their bodyweight. They do however need this amount of reserves as the birds need to draw on these whenever winter weather makes it impossible for them to search for food, for example when there are heavy storms. By February the birds have generally exhausted their fat reserves. In reindeer and musk oxen the quantity of fat reserves also determines whether a female is fertile and able to produce offspring.

The Arctic ground squirrel *(Urocitellus parryii)* is among the few polar species that sleep through the winter. Despite the fact that the squirrels' body temperature drops down to as low as minus three degrees Celsius, their blood does not freeze and their organs and tissues are not damaged by ice crystals. To avoid death by hypothermia the animals wake up every three weeks from their state of torpor and begin to shiver for one or two days which raises their body temperature back up to 34 to 36 degrees Celsius. In the course of this process the squirrels burn a lot of fat which they had accumulated during the short summer. They then fall back into hibernation.

In polar bears, only pregnant females spend the winter in a snow den where they also give birth to their cubs. Juvenile bears and adult males are more or less active throughout the winter; after all they need to accumulate a great deal of body fat as long as the sea ice allows them access to the seal territories.

4.11 > An Arctic ground squirrel is curled up in its den on a bed of moss and sleeps through the winter which can last for seven to nine months. The animals are active only during the short Arctic summer.

Since seals moult once a year they too face a regular period of fasting. During this time the animals stop searching for food and reduce their metabolism by half. They generate body heat and kinetic energy solely by drawing on their fat reserves. In contrast, Arctic foxes and stoats do not solely rely on their accumulated body fat. They also hoard food, a task that keeps them busy from September to November. Some animals hide their kills in many different places while others store them all in one place. The biggest known hoard of an Arctic fox contained 136 seabirds which the predator had apparently taken at a breeding colony. For stoats there are reports of individual animals accumulating as many as 150 killed lemmings in winter stores.

Adaptations to light conditions

One of the polar regions' unique characteristics is the change between long periods of daylight in summer (polar day) and long periods of darkness during the winter (polar night). In the interim periods, light conditions change so fast that in places such as Spitsbergen or in northern Greenland day-length increases or decreases by 30 minutes per day. These changes require constant behavioural adaptations on the part of the animals, as the available light not only determines the animals' daily rhythm but also their annual calendar and thus the timing of important events such as mating, hibernation or moulting. This is true not only for organisms residing in the southern and northern polar regions but also for the animals in the rest of the world.

The animals' internal clock is regulated by means of biochemical processes which commence when information on light conditions is received by special light-sensitive neurons in the eyes' retina. The signals are transmitted along neural pathways, first to the suprachiasmatic nucleus and subsequently to the pineal gland. The former is a nucleus within the brain; it is situated in the hypothalamus and is, just like an internal clock, responsible for controlling the circadian rhythms of mammals. The pineal gland is located at the back of the midbrain. Only during periods of darkness does it produce the hormone melatonin which is then released into the blood and the cerebrospinal fluid. This means that with decreasing night length, the amount of melatonin in the body also decreases and in turn so does its process-inhibiting impact.

Simply put, melatonin synchronizes all the processes taking place in an animal's body and adapts its internal clock to the current time of day and season. However, polar species display a special characteristic in this respect. While most animals outside of the Arctic and Antarctic are active during the day and rest at night, Arctic and Antarctic species adapt their behaviour to the current light phase.

Arctic ptarmigans are a good example. During spring and autumn when the sun rises and sets they search for food in the morning and evening, just like many other bird species. However, during the phases of constant darkness and constant brightness respectively the birds are basically searching for food around the clock except for some breaks. This same pattern of behaviour has been observed in reindeer on Spitsbergen and in Adélie penguins. Similarly, it is known that male emperor penguins do not have strikingly high levels of melatonin even during the polar night. The animals thus do not display typical diurnal rhythms during the polar day and polar night.

It is easier for reindeer than for other animals to search for food even during long periods of darkness as they are able to detect light in the ultraviolet spectrum. This ability provides them with a crucial advantage. Since snow and ice largely reflect incoming ultraviolet light, the animals see the landscape as a light-coloured surface. In contrast, anything that absorbs UV light appears black to them. This includes lichens, the reindeer's main food source during the winter. But white fur (polar bears) and the fur of wolves also only reflect a small portion of UV light. The reindeer can therefore detect potential attackers at an early stage which greatly increases their chances of survival.

Scientists also assume that the UV light allows the animals to detect the texture of a snow surface, since the proportion of reflected UV light changes with the snow cover's physical characteristics. Presumably the herds are able to see at first glance whether it is worth searching for food in a particular place, or whether they would be better off taking a little detour because the snow in a particular location is too harsh or too soft to cross.

Changing colour at the start of winter

The changing light conditions also signal the start of the typical moult which gives Arctic foxes, Arctic hares, stoats and other animals their mostly grey or brown summer coat and their white winter coat. In the temperate and polar latitudes of the northern hemisphere there are 21 species of mammals and birds at present that change colour with the seasons. This means that the animals have to grow an entirely new coat or plumage twice a year. While the evolution of seasonal colour changes is not yet fully understood, presumably the species developed this ability independently of each other. Interestingly, however, different species in a region change their colour almost at the same time and hold onto their winter plumage or winter coat for a similar period, in alignment with the general local timing of the first snowfalls and the length of time the snow cover tends to persist. Species living in areas with highly variable or patchy snow cover have also adapted their coat colour to these conditions. Their winter coat or plumage contains a number of pigmented hairs or feathers and generally appears speckled whitish-brown or whitish-grey.

Scientific research has been conducted into the purpose of the colour change. The results indicate that it primarily serves camouflage and thermoregulation. A white coat or plumage in winter is highly advantageous for both predators and prey. If the landscape is covered in snow, both groups are harder to be spotted by their respective adversaries. The former has greater prospects of catching food while the latter has a greater chance of survival. For this reason, scientists consider a species' ability to camouflage themselves as being one of the primary drivers in the evolution of mammalian coat colour.

However, an animal can only optically become one with its environment if the moult and the onset of snowfall or snowmelt take place more or less at the same time. If the onset of winter is delayed or if the snowmelt starts much too early in the year, the animals have the wrong coat colour and their evolutionary advantages turn into disadvantages. It is for this reason that species which change their coat colour face a greater threat to their existence from climate change than animals that maintain their coat colour.

Scientists consider birds to be an exception to this rule as often their self-awareness is so strong that they notice the discrepancies between the colour of their environment and their plumage respectively and adapt their behaviour accordingly. Rock ptarmigan and white-tailed ptarmigan,

4.12 > Rock ptarmigan, Arctic hare, stoat and Arctic fox are among the world's 21 animal species that change the colour of their coat or plumage with the seasons. This makes it harder for both predators and prey to be spotted and increases their chances of survival. Often the winter coat or winter plumage also has better insulating properties compared to the summer coat or plumage.

for example, only rest in locations where the dominating ground colour matches that of their plumage. And researchers in Canada observed ptarmigans that deliberately dirtied their plumage when the snowmelt began too early and the birds in their clean white winter plumage were at risk of being detected too easily.

Another effect of the change from summer to winter coat is that the animals improve their furs' insulating properties. Colourless or unpigmented hair tends to be somewhat broader than pigmented hair or it contains a greater number of air-filled chambers, thus improving its insulating qualities. Additionally, the white winter coat is often longer and denser than the summer coat. This is true for the Arctic fox, the northern collared lemming *(Dicrostonyx groenlandicus)* and the Djungarian hamster *(Phodopus sungorus)*.

Just like many other processes, the moult is triggered by changes in melatonin concentrations. When melatonin increases in the autumn, signals are transmitted to the pituitary gland which produces the growth hormone prolactin, among others. This hormone in turn regulates hair growth and other functions. When the prolactin concentration rises in the spring, collared lemmings and Arctic hares lose their winter coat and commence their search for partners. However, if the production of this hormone is suppressed, Arctic foxes, lemmings and other animals produce their light-coloured winter coat. In experimental studies, mammals whose prolactin production was suppressed kept their winter coat throughout the entire year, independent of day-length.

Vascular plants
The term vascular plants is applied to all ferns and seed-producing plants, as these have internal vascular tissues which distribute resources through the plant.

But melatonin also inhibits the production of the pigment melanin which gives skin, feathers and eyes their colour. In animals with seasonal coat colours, a high melatonin concentration thus directly results in the growth of a white winter coat. There is less of an understanding as to how day-length and hormones regulate the moult and change of plumage in birds. In part this is due to the fact that birds have at least three "internal clocks". Information regarding changing day-length is processed not only in the pineal gland, but also in the hypothalamus and in the eyes themselves. Moult and reproduction are coordinated such that the change in plumage does not commence before the breeding period has finished.

In contrast to day-length, environmental factors such as temperature and snowfall only have a limited impact on the change in coat or plumage. Studies have shown that low autumn temperatures accelerate the growth of winter coats or plumage in mammals and birds respectively. Moreover, ptarmigans were shown in experiments to produce a darker winter plumage if they were kept at higher temperatures. In contrast, a cold spring with plenty of snow slowed down the change from winter to summer colour. The moult, however, is solely triggered by day-length.

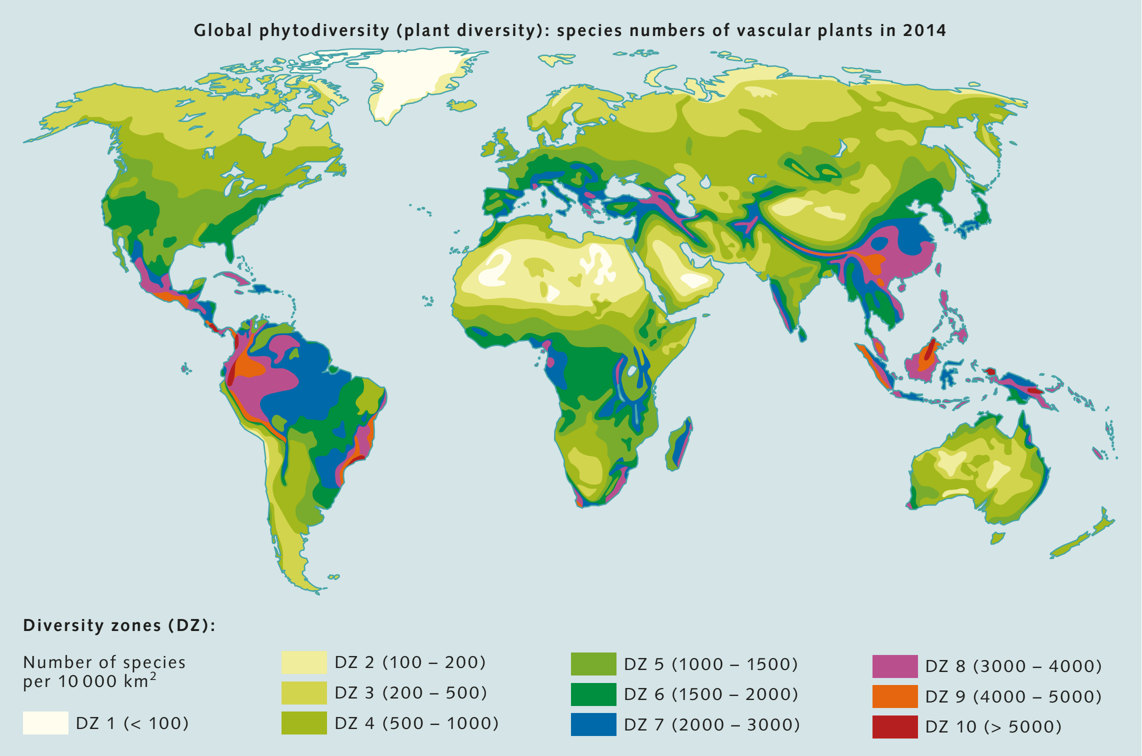
The flora of the polar regions

Despite their extreme climate, the north and south polar regions host a remarkably rich flora in places. For example, in the Arctic researchers have counted almost 100 different species of vascular plants, mosses and lichens in an area of 25 square metres, making the site examined roughly as species-rich as the most species-rich grasslands of the temperate and subtropical latitudes. Compared to tropical rainforests, however, the polar regions are indeed species-poor. This is primarily due to the low temperatures, the short growing season, the lack of nutrients, the difficulty of rooting in permafrost soils, and extreme weather events in the Arctic such as the typical spring floods. Moreover, growing conditions for plants in the polar regions are often greatly divergent between locations. On the Siberian Taymyr Peninsula, for example, a mere 500 kilometres separate the sub-Arctic with its relatively lush growth from the polar desert of the High Arctic in which only few plant species survive.

The vegetated lowlands of the Low Arctic are also termed tundra. This term is derived from the word *tūndar* which, in the language of the Saami, the original inhabitants of northern Scandinavia, means "a plain devoid of trees". While in addition to grasses and vascular plants willow, birch and alder, all of which have tree relatives further south, do indeed grow in the tundra, they do not grow up high in the classic tree shape but form creeping scrub or mats just above the ground, not least in order to escape the icy winds. In the northernmost areas of


4.13 > Blueberries in the Arctic ripen only towards the end of summer. The Inuit say it is incredibly laborious to gather them as the plants grow so closely to the ground that one has to crawl through the tundra on all fours in order to pick them.

4.14 > Vascular plant species diversity is highest in the tropics and declines with increasing latitude. In the Arctic, the regions relatively species-rich are primarily those that were not glaciated during the past ice ages.



Global phytodiversity (plant diversity): species numbers of vascular plants in 2014

Angiosperms and gymnosperms

Angiosperms are flowering plants and are characterized by the enclosed ovary, which contains and protects the developing seeds. In contrast, gymnosperms are characterized by the unenclosed condition of their seeds. Gymnosperm seeds develop lying unattached on the surface of individual carpels. European larch and Scots pine are well-known gymnosperms.

Siberia, on the eastern and western coasts of Greenland, in the Canadian Arctic Archipelago and in the north of Alaska the areas of tundra grade into the High Arctic with its thin vegetation cover dominated by lichens, mosses and dwarf vascular plants. To its south, the tundra is in many areas bordered by the subarctic krummholz zone consisting of climatically stunted and distorted trees.

Vascular plant species diversity in the polar regions declines with increasing proximity to the poles. In the Arctic, the current vegetation of which has only developed over the past three million years, an estimated 900 species of mosses and 2218 species of vascular plants have been identified. Almost all of the vascular plants are flowering plants (angiosperms). Gymnosperms, in contrast, are rare in the Arctic and where they occur their species diversity tends to be low.

The majority of Arctic plants are considered to have a circumpolar distribution. Nonetheless there are major differences between different regions in terms of their species diversity and composition. While a mere 102 species occur in the northernmost part, the High Arctic, the southern tundra regions host more than 20 times that number of species. Approximately five per cent of Arctic vascular plants are endemic species, which means that they occur nowhere else but in the Arctic. Those species are mainly forbes and grasses.

The diversity of the Arctic flora is also supported by herbivores. When researchers excluded grazing animals such as geese, lemmings, musk oxen and reindeer from certain areas as part of a study, large amounts of plant litter accumulated, insulated the soil and led to the soil not thawing to a sufficient depth in the summer. Vascular plants could no longer develop a sufficient root network and disappeared. Mosses now grew in their place. Moreover, the herbivores' faeces provide badly needed nutrients, as nitrogen and phosphates are scarce in Arctic soils.

Compared to the Arctic, the Antarctic flora is truly species-poor. In its continental zone, defined by biologists to include the few ice-free areas of continental Antarctica and the eastern side of the Antarctic Peninsula, only a small number of 40 to 50 different species of lichens and mosses thrive. These generally grow in rock crevices or depressions between stones and mainly on dark rocky ground which absorbs most of the incoming solar energy and radiates heat. Most of these lichens are truly extreme survivalists. Even at a temperature of minus ten degrees Celsius they can still photosynthesise and survive even under conditions of strong and persistent desiccation and extreme cold. Some of the species occur even in the ice-free Antarctic dry valleys of Victoria Land.

4.15 > Biologists differentiate three vegetation zones in the terrestrial north polar region. The High Arctic is the northernmost zone. It borders on the tundra of the Arctic lowlands, and the tundra in turn borders on the northern margins of the boreal zone.

The western side of the Antarctic Peninsula and the nearby islands offer a warmer and moister climate and thus more favourable conditions for plants. In this zone, termed the maritime Antarctic, two vascular plant species can be found – Antarctic hair grass *(Deschampsia antarctica)* and Antarctic pearlwort *(Colobanthus quitensis)*. The bulk of the Antarctic vegetation, however, is composed of cryptogams. Some 100 species of mosses have been recorded as well as 750 species of lichens and an estimated 700 species of terrestrial and oceanic algae. The number of fungus species has not been determined.

Fighting the cold

With increasing proximity to the poles, conditions for plants deteriorate, or to put it differently, physical and chemical factors which limit plant dispersal have increasingly greater impact. These factors include, for example, the length of the growing season, the duration and intensity of frost periods, and the degree to which the plants are exposed to wind. However, the plants' chances of survival are also linked to available resources. Whether they are in the tropics or in the polar regions, plants can only exist if their carbon budget is positive, which means they must be able to sufficiently photosynthesise in order to grow and store energy reserves in the form of glucose or starch. To this end the plants require sufficient amounts of heat, water, light, carbon dioxide and nutrients as well as oxygen. The latter is required in particular by plants growing in wetlands or swamps.

The polar regions rarely offer ideal conditions for plant growth. The Arctic flora has therefore developed a range of adaptation mechanisms that allow them to tolerate conditions of nutrient deficiency, cold and darkness and to survive with little or no harm extreme events such as prolonged snowfall or spring floods. These adaptations include the following:

- slow, resource-conserving growth,
- a more brown than green coloration,
- a squat stature,
- heat-optimizing characteristics such as fine hairs or special flower shapes,
- mechanisms to protect cells from frost damage,
- a large number of important enzymes enabling photosynthesis even in adverse light conditions,
- nutrient recycling,
- major energy reserves in the root system, and
- the opportunity of asexual reproduction at locations where conditions are such that sexual reproduction does not work.

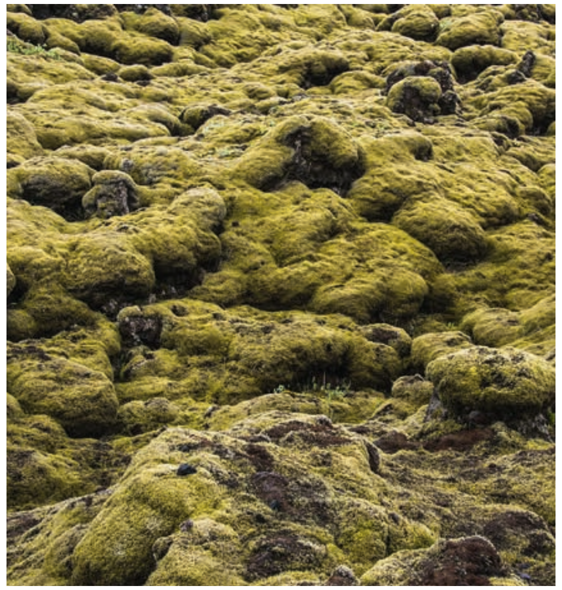
Small is beautiful

Polar plants particularly like to settle in sheltered locations where they are not exposed to the full forces of the wind, ice and cold. A second important survival strategy is to grow slowly and reduce energy consumption especially at times of low resource availability. This approach is known as the Montgomery effect, named after Edward Gerrard Montgomery, a scientist at the University of Nebraska Agricultural Experiment Station (USA). When conducting experiments involving a variety of cereal cultivars he found that in locations offering low environmental resources slow growth does indeed confer ecological benefits onto plants. In the Arctic, for example, the summer and therefore the growth phase is so short that plants such as the Arctic wintergreen *(Pyrola grandiflora)* growing in Iceland and Greenland take several years to grow from the initial sprout to a mature plant capable of seed production. This also explains the longevity of many plants in the polar regions.

The tiny pygmy buttercup *(Ranunculus pygmaeus)* is a species that has perfected prudent resource use. It often grows surrounded by mosses in the vicinity of glaciers, streams or snow drifts and survives even if it is occasionally covered by so much snow in the winter that this snow does not melt in the course of the following summer, resulting in the plant missing out on an entire cycle of growth and reproduction. Other species are so thrifty in their resource use that they can persist for even two or three years in series underneath a snow cover. These include Alpine bistort *(Polygonum viviparum)*, mountain sorrel *(Oxyria digyna)* and polar willow *(Salix polaris)*.

The small and squat stature of many polar plants is not only a result of their drawn-out growth. Plants forming thick ground-covering carpets instead of having their leaves and flowers shoot upwards will escape the icy Arctic winds. The air held inside these carpets or cushions is swirled to a lesser degree and is more easily warmed by the sun. In this manner the carpeting plants create their own microclimate, the temperature of which may reach 25 to 30 degrees Celsius on summer days when the ambient temperature at a height of two metres is a mere eight degrees Celsius. The plants inside the carpet thus enjoy optimum metabolic conditions at such times.

In order to grow and flower during the short and cool summer, polar plants also employ strategies which in warmer regions would lead to immediate death from heat stress. One of the strategies is coloration. Darker colours



4.16 > Mosses colonizing a lava field in Iceland. The Arctic is home to some 900 species of mosses. They can mostly be found in Arctic wetlands and on snowbanks.

4.17 > Alpine bistort ***(Polygonum viviparum)*** is one of the Arctic plant species that can persist underneath a snow cover for periods of more than two years.

4.18 > Antarctic hair grass ***(Deschampsia antarctica)*** is one of the two vascular plant species that are native to the Antarctic continent.

4.19 > The white petals of the flowers of glacier buttercups ***(Ranunculus glacialis)*** reflect sunlight towards the centre of the flowers which makes them very attractive to insects.

4.20 > The white cotton-like plumes of cottongrass are a familiar sight in Arctic wetlands. However, these are not the flowers but only develop along with the seeds. The long perianth bristles form white tufts which also protect the seeds from the cold.

absorb a greater amount of solar radiation than lighter colours. This explains why the vegetative cover in many of the Arctic areas appears predominantly brown instead of green. This is particularly true for plant communities on Arctic beaches where the growing season is particularly short.

Moreover, plants like the glacier buttercup *(Ranunculus glacialis)* are able to align their leaves and flowers at an optimum angle to the sun. Its initially white flowers then function like little parabolic dishes which direct the incoming sunlight directly to the reproductive organs at the centre of the flower. This increases the air temperature inside the flower which in turn results in the reproductive organs developing at a faster rate and in the flowers attracting a greater number of insects. Following pollination the glacial buttercup closes its flowers and the petals turn red, allowing the flower to absorb a greater amount of solar radiation, the heat content of which in turn protects the seeds developing inside the flower.

Other Arctic plants create their own “greenhouse”. Female polar willows *(Salix arctica)*, for example, grow fine downy hairs on their leaves and along their inflorescences. This downy cover traps an insulating layer of air close to the leaf surface. The hairs also reduce the leaf surface area which normally would be subject to heat loss as a result of evaporative cooling. The downy hairs so efficiently protect the little willows that the temperature of the leaves may be up to eleven degrees Celsius higher than the ambient temperature.

Northern plants also avoid growing their roots deep into soils where much of the ground stays frozen throughout the year and where meltwater accumulates. Instead they take root in the shallow layer of topsoil which is the first to melt in springtime and generally tends to be waterlogged only for short periods. At the end of the summer, trees and shrubs drop their needles and leaves and overwinter in a dormant bud stage. Before they go dormant, however, they cover their buds in a wool-like substance in order to protect them from the frost.

Many Arctic plant species defy the freezing cold winter temperatures by moving water, among other substances, from their cells into intercellular spaces. In this manner the plants reduce the risk of ice crystals forming inside of cells and damaging these. The plants simultaneously strengthen the cell membranes with certain types of sugars and proteins; the membrane’s lipid composition also changes. Special enzymes prevent the cells from suffering damage due to dehydration. However, these cellular frost protection mechanisms are not activated year-round. They only play a role when temperatures drop at the end of summer and the plants are acclimatizing. At the height of winter most plants are so well protected from frost damage that some even survived laboratory trials as part of which they were briefly dipped into liquid nitrogen at a temperature of minus 196 degrees Celsius.

However, problems arise when unusually warm periods and severe frost alternate during the winter or when normally snow-covered areas suddenly become free of snow. These kinds of conditions can damage even the hardiest of Arctic plants. Nonetheless, in most cases the plants will be able to compensate for such damage by growing new leaves and shoots in the spring.

Making the most of the short summer

Plants need active enzymes in order to take up carbon dioxide, to photosynthesise and to generate energy reserves in the form of glucose and starch. Cold-adapted plants of the polar regions contain a particularly high level of active enzymes. Large quantities of the enzyme RuBisCO (Ribulose-1,5-bisphosphate carboxylase/oxygenase) allow the Arctic flora to uphold metabolic activity even at lower temperatures. But even polar vascular plants cannot grow at subzero temperatures. The plants must wait for the short summer in order to develop leaves and flowers and they must be able to make optimum use of this short period. The cells of cold-adapted plants contain particularly high numbers of mitochondria which, as the cells’ “power plants”, are responsible for energy generation. With their help the plants increase their metabolism to maximum levels during the summer. Not only do they make optimum use of the 24 hours of daylight but they are also able to photosynthesise in unfavourable light conditions.

This strength, however, makes the cold-adapted plants susceptible to heat stress. If the ambient temperature rises to greater than average levels, both metabolism and cellular respiration increase well beyond healthy levels. The plants then swiftly use up all their energy reserves and suffer damage. This explains why polar plants of the Arctic do not spread further south. It also highlights one of the mechanisms by which climate change poses a risk to polar plants. Rising temperatures increase the probability of cold-adapted plants succumbing to exhaustion.

Searching for nutrients

Some plants actively seek out resources so as to have sufficient amounts of nutrients and light at their disposal during the short growing period. They develop small shoots or runners above or below ground which they use to tap into light and nutrient sources away from their original location that are crucial to their survival. This strategy can offer the plants clear locational advantages, as a comparison between two closely related cottongrass species has shown, both of which grow in Arctic wetlands.

Common cottongrass *(Eriophorum angustifolium)* develops runners and actively searches for minerals, an ability that allows the plants to survive in the very wet parts of the marshes. Their runners tolerate stagnant water and allow the species to spread into flooded areas. In contrast, the hare's-tail cottongrass *(Eriophorum vaginatum)* does not send out shoots into its nearby environment. It grows instead as tussocky grasses and thrives in particular in the drier locations where there might be significant water level fluctuations.

The energy reserves produced by the plants by means of photosynthesis during the short summers tend not to be invested into the development of new leaves but are mostly put into subterranean storage in the form of starches in the plants' roots. Therefore the root systems of Arctic plants are generally larger than those of plants of temperate or tropical latitudes. It makes sense for the plants to accumulate significant reserves in the north polar region with its highly variable weather conditions; there is always a possibility that they might miss out on one or even two growing periods while buried under snow, a time during which they must live on their reserves. It is for this reason that plants of the tundra such as bog-rosemary *(Andromeda polifolia)* store up to 75 per cent of their energy reserves in their roots.

Nutrients such as nitrogen, phosphorus and potassium are also particularly valuable to polar plants. Plants such as the dwarf birch *(Bitula nana)* have therefore found ways to recycle them once they have taken up and processed such elements. Shortly before the birch drops its leaves at the end of summer the plant withdraws a major proportion of the nutrients stored in these leaves back into the more permanent plant body. Hare's-tail cottongrass employs the same mechanism; it can recycle 90 per cent of the phosphorus contained in its leaves, which means that in the springtime the plant only needs to newly take up ten per cent of its phosphorus requirements from the soil.

Two ways to reproduce

Most animal species rely on sexual reproduction for their species' survival. In contrast, plants often have the option of asexual reproduction. They may form runners, branches or even seeds, with the latter being produced in the absence of classic pollination (agamospermy). These strategies have allowed several plant species at home in the Arctic to persist for centuries or even millennia, one example being Arctic sedges such as *Carex ensifolia*.

Sexual reproduction in vascular plants may fail either because of a failure to develop flowers or because pollination could not take place. In some species the latter may be caused by even just a brief cold spell. In the northern range of the American dwarf birch *(Betula glandulosa)*, for example, only 0.5 per cent of birch seeds germinate. In order to survive in these regions the species has no choice but to resort to asexual reproduction.

In the springtime shortly after the snowmelt the tundra suddenly bursts into bloom. This spectacle is primarily caused by perennial plants. With very few exceptions there basically are no annual plant species in the polar regions. In order to develop flowers in such a short timeframe, Arctic plants need flower buds which have already been initiated in the autumn and which can immediately kick into action following the snowmelt.

The many flowering plant species of the Arctic are primarily pollinated by flies, which is not very surprising as there are hardly any bees north of the polar circle. When scientists in Greenland took a closer look at the insects responsible for pollinating mountain avens *(Dryas octopetala)*, a characteristic plant of the Arctic, they counted a total of 117 different insect species which visited the plant. However, pollination was primarily performed by a single species, a small relative of the housefly called *Spilogona sanctipauli*.

To spend the winter in the form of a seed in the soil is a globally widespread and highly successful survival strategy of plants – this is no different in the polar regions. When scientists studied the flora of Spitsbergen they found that 71 of the 161 native plant species produced seeds in order to ensure the survival of the species. The same strategy is employed by the only two Antarctic flowering plant species. Plant seed longevity varies around the globe. While the seeds of some species persist in the soil for less than a year, some Arctic plant seeds display surprising levels of resilience. As part of scientific studies, seeds of the sedge species *Carex bigelowii* which were approximately 200 years old were still able to germinate; and in Alaska seeds of the small-flowered woodrush *(Luzula parviflora)* germinated after an estimated 175 years in the ground. If one day environmental conditions were to rapidly deteriorate, these species would therefore be in a position to persist as seeds in the soil for several decades or even centuries, and to germinate once conditions have become more favourable.

Over the past two to three million years, the flora of the polar regions has displayed a remarkable capacity to survive and adapt, and especially in the Arctic a rich diversity of species has emerged. Global warming will now pose new challenges for the cold-adapted flora, and the degree to which the polar biodiversity will be able to persist is uncertain.

4.21 > Autumn in the Arctic: A yellowish-orange carpet of shrubby willows and dwarf birches covers this headland in the Canadian Arctic. This far north the American dwarf birch *(Betula glandulosa)* primarily reproduces asexually.

Marine life

> The productivity of the polar seas and their species diversity verge on the miraculous. To an outsider, living conditions in the Arctic and Antarctic Oceans seem anything but inviting. The constantly cold water inhibits the growth of cold-blooded organisms and slows their every movement. Food is available only during the brief summer – although it is then abundant. But the inhabitants of the polar seas – especially the dwellers of the Antarctic – have developed unique adaptation mechanisms to compensate for these limitations.

In the rhythm of light and ice

Like the land areas of the polar regions, the seas are also classed as extreme habitats. The Antarctic and Arctic Oceans have the coldest and most constant water temperature of all the world's oceans. This temperature is below zero degrees for most of the year and seasonal fluctuation is usually less than five degrees Celsius. In very southerly ocean regions such as the McMurdo Sound, a bay that forms part of the Ross Sea in the Antarctic, the difference between summer and winter temperatures is in fact less than half a degree Celsius. The inhabitants of this region must therefore cope with very cold ambient temperatures throughout the year. For most of the time the water temperature is minus 1.8 degrees Celsius. Furthermore, seasonal changes have a more marked effect on the polar seas than on any other ocean: in summer the sun never sets, while in winter darkness reigns for months on end.

This switch between polar day and polar night has a profound impact on life in the Arctic and Antarctic Oceans. Sea ice forms as the days shorten, so that in winter it covers much of the ocean surface; in summer the ice melts again, retreating to a minimum area. The ebb and flow of light and sea ice determine the rhythm of life in the polar regions. Where the sea ice breaks up in summer, sunlight at last penetrates the upper layers of water and stimulates algae growth. At the same time, the melting floes release microorganisms and other life-forms associated with the ice; these disperse in the water, along with trace elements such as iron that have been encased in the ice or deposited on its surface in the form of dust over the winter.

In the spring and summer, sunlight, iron and other water-borne nutrients such as nitrogen, phosphorus and silicon compounds trigger large-scale algal blooms that provide the basis for the food webs of the polar oceans. In coastal waters in the Antarctic, algal density can peak at a level of 30 milligrams of chlorophyll per cubic metre of water. In winter, by contrast, there are so few algae in these same places that the water's chlorophyll content may fall to less than 0.01 milligrams per cubic metre. In no other ocean are seasonal differences in biomass production so large. In autumn and winter the formation of sea ice inhibits life in the Southern Ocean. When the sea surface cools and turns to ice, key nutrients such as iron have usually been used up by algal growth in the summer. Any substances that remain sink to the sea floor, partly as a result of the thermohaline circulation of the water masses. This means that virtually no food is left in the upper metres of the water column. Algae stop growing and primary production ceases. Moreover, the sea ice shields the water column from the wind and thus prevents intermixing of the upper water layers. As a result of this lack of eddying, algae, faeces and other particles suspended in the water column fall to the sea floor, thereby drastically reducing the nutrient content of the column.

For most of the inhabitants of the polar seas, the seasonal succession of light and ice means that periods of abundance constantly alternate with periods of hunger. In addition, many organisms – particularly those that live on the bottom of the shelf seas – are always in danger of having their habitat destroyed by drifting icebergs or sea ice floating in the shallow waters. An iceberg ploughing across the sea floor in the Antarctic kills more than 99.5 per cent of the established macroorganisms and more than 90 per cent of the smaller meiofauna. In areas in which icebergs are plentiful this can happen more than once a year. In consequence, the biotic communities in these disturbance zones are usually very young and colonize the sea floor only patchily.

Meiofauna
Meiofauna, also known as mesofauna, are a major category of benthic fauna. The term covers all bottom-dwelling organisms of between roughly 0.05 millimetres and one millimetre in size. Smaller organisms are classed as microfauna, while larger ones up to 20 millimetres in size fall under the heading of macrofauna.

A question of iron

Although the marine fauna of the Arctic and Antarctic have much in common with each other, they are not identical. This is partly because of differences in the supply of nutrients and trace elements in the two regions. In the far north, rivers carry large quantities of suspended material into the marginal seas, thus providing the Arctic Ocean with the iron that is vital to living things; the deep south, by contrast, lacks such a reliable source of iron. Although the water masses of the Antarctic are nutrient-rich, they suffer from an almost universal lack of iron. In consequence, algal blooms form mainly in two areas: firstly, in the coastal waters and polynyas (areas of unfrozen sea within the ice pack), where iron comes from sources such as glacier meltwater, and, secondly, on the edges of the continental plate, where iron-rich water wells up from the depths. The largest of these upwelling zones stretches eastwards from the tip of the Antarctic Peninsula to South Georgia. It is a hotspot of life, home to the largest concentrations of krill in the Antarctic and a magnet for krill hunters such as whales, penguins and seals.

By comparison, the upper water layer of the central Arctic Ocean is relatively nutrient-poor. The summer ice melt and the pronounced stratification of the Arctic water masses as a result of the large quantities of freshwater discharged by rivers prevent deep, nutrient-rich water rising to the surface. Brief, intense algal blooms in the spring and summer therefore occur mainly near the edge of the ice and in the marginal seas. The Barents Sea, Chukchi Sea and Bering Sea are among the most pro-

4.22 > Elephant seals, together with king penguins and other seabirds such as petrels and albatrosses, line the shore of Saint Andrews Bay on the north coast of South Georgia. Here the penguins form breeding colonies of up to 100,000 birds.

4.23 > Copepods not only make up the majority of marine zooplankton – with around 13,000 species, they are also the most species-rich group of crustaceans. Polar species are usually somewhat larger and more nutritious than their relatives in the mid-latitudes.

ductive marine ecosystems in the world, providing so much food for bottom-dwellers, fish, seabirds, seals and whales that huge colonies of these creatures can occur.

Despite this, animal numbers in the Arctic are often only a fraction of the size of Antarctic populations. For example, in the area around the North Pole and the adjacent sub-polar regions there are just 13 bird species with a total population of more than a million, while in the south there are 24 polar and sub-polar bird species. The most abundant seal species likewise lives in the Antarctic: it is calculated that there are between 50 and 80 million crabeater seals *(Lobodon carcinophaga)* in the region, although the vast extent of their habitat means that population estimates are uncertain.

The large numbers of birds, seals and whales in the polar seas at one time led scientists to assume that more biomass is produced and passed on in the food web in these regions than is the case at lower latitudes. This was attributed to short food chains formed of a few key organisms. With regard to the Antarctic it was thought that almost all life hinged on diatoms photosynthesizing and being eaten by Antarctic krill, which were in turn hunted by all the larger animals such as fish, penguins, seals and whales.

This simplified point of view is outdated. We now know that the range of primary producers in the polar seas – in this case predominantly the algae – is just as diverse as in the mid-latitudes. Microbes, plankton and other microorganisms interact in complex ways. In addition, it is now recognized that, although krill undisputedly remains one of the key species, there are many feeding relationships in the Antarctic in which it plays no part.

Consideration of the food web in the two oceans reveals two striking features. Firstly, in the polar seas there are relatively few species that serve as food for the large predators. For example, 80 to 90 per cent of the zooplankton in the Arctic consists of fatty copepods, which form the most important link between the primary producers and larger consumers such as fish and baleen whales. In the Antarctic, this role is performed by krill, amphipods and copepods. Secondly, the hunters and consumers of the Antarctic pursue different prey from those of the Arctic. While seals, whales and seabirds in the Arctic Ocean eat mainly fish and organisms that live on the sea floor, the large predators of the Antarctic Ocean feed largely on krill and fish such as the Antarctic silverfish *(Pleuragramma antarctica)*. Sharks, walruses and whales that search for food chiefly on the sea floor are completely absent from the Antarctic.

The survival tricks of cold-blooded sea-dwellers

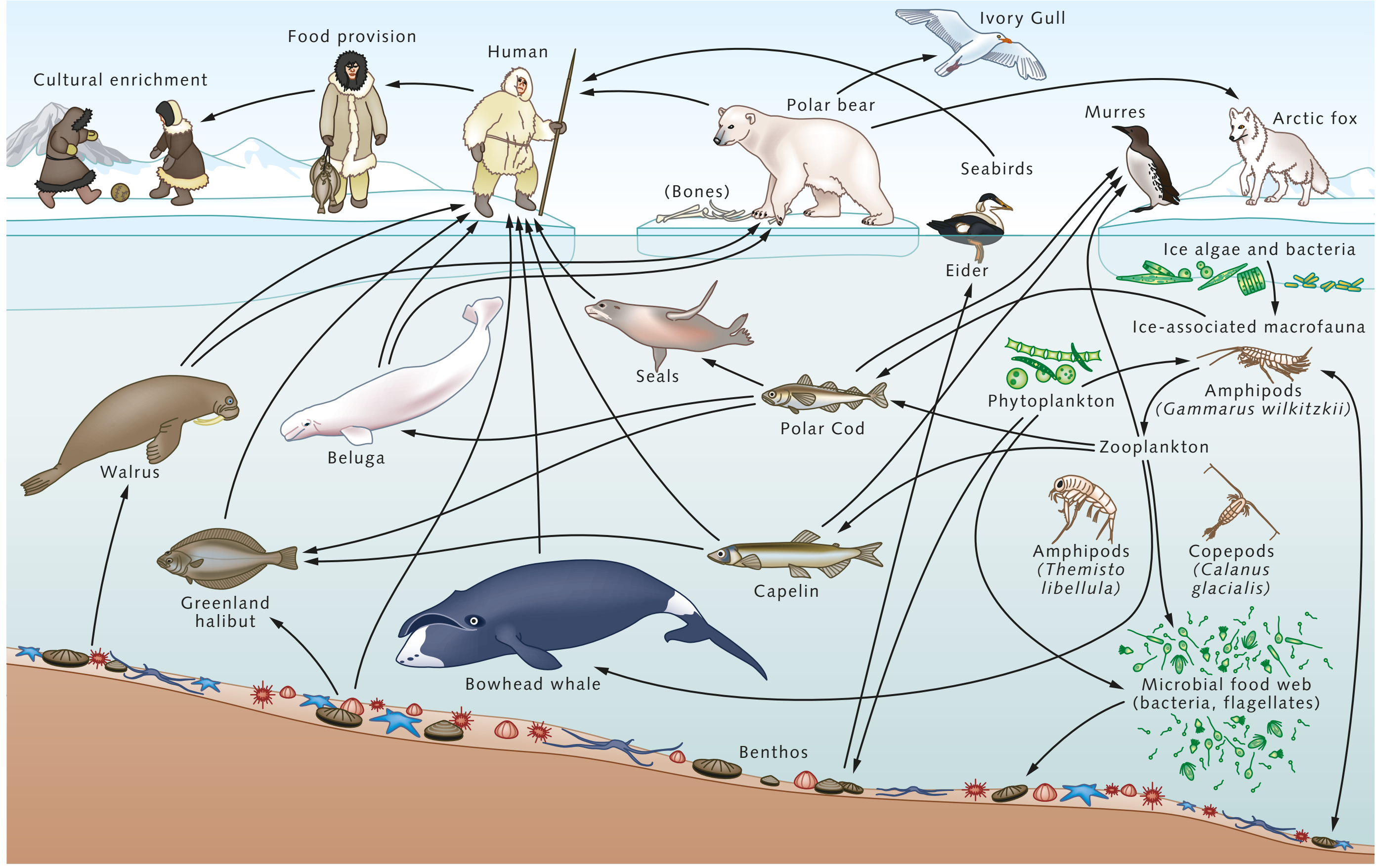
The fauna of the polar seas consists largely of cold-blooded creatures which over millions of years have developed unique mechanisms for adapting to their extreme living conditions. However, because of the geographical isolation of the Antarctic and its longer glacial history, these mechanisms are more marked there than in the Arctic. Notable adaptive mechanisms in the cold-blooded creatures include:

- slower growth, late sexual maturity,
- reduced activity,
- production of antifreeze proteins (especially in fish),
- reduction in red blood cells (also mainly in fish),
- incorporation of unsaturated fatty acids into cell membranes,
- weight savings by doing without calcium deposits in scales and skeleton,
- gigantism,
- smaller clutches with large eggs that contain food reserves to support the growth of the larvae, and
- live births and attentive care of the young.

Temperature and lack of food as brakes on growth

Cold has a persistently adverse impact on the lives of cold-blooded sea creatures. Among other things, it affects their respiration and muscle function and hence their ability to move. It also slows their growth and development, and in consequence there is considerable similarity between the life cycles of polar species. Life in the cold oceans proceeds very slowly, and each developmental step takes longer than in the mid-latitudes. For example, the embryonic

4.24 > Ice algae and free-swimming phytoplankton in the water form the foundation of the food web in the Arctic Ocean. Using sunlight, carbon dioxide and nutrients, these organisms produce biomass that provides nourishment for all consumers, from zooplankton to bottom-dwellers, fish, birds, sea mammals and ultimately humans.



The Methuselah of the North Atlantic

The waters around Iceland and Greenland contain sharks that are thought to have been hunting there at the start of the French Revolution in 1789 – 230 years ago. This hypothesis emerged from a study conducted in 2016 in which researchers determined the age of 28 Greenland sharks *(Somniosus microcephalus)*. The oldest female, which was 5.02 metres long, was found to be at least 272 years old but could have been as old as 512. It was impossible to pinpoint her age more precisely, because Greenland sharks are cartilaginous fish and hence have no bony vertebrae or fin spines whose growth rings the researchers could have counted. Instead, the scientists had to look at the sharks' optical lenses, which are formed at the embryonic stage, and use radiocarbon dating to measure the carbon isotope content. The findings made headlines, because no other vertebrate is known to live as long as these giants of the Arctic Ocean.

Greenland sharks are very rarely seen in the wild. They are predators that prefer regions in which water temperatures are below five degrees Celsius; on their search for carcasses or living prey they roam the coastal waters and deep seas of the Arctic and North Atlantic. To save energy, though, they meander through the Arctic waters at a sluggish pace, swimming at an average speed of 30 centimetres per second (1.08 km/h). They are thus significantly slower than most other sharks, but this does not deter them from hunting fish, seals and beluga whales. The animals reach sexual maturity at the age of 156 (± 22). Their young hatch from the egg while still inside the mother's body; at birth they are thought to be about 40 centimetres long. Since they grow at a rate of less than a centimetre a year, one can only speculate on the age of the Greenland sharks up to 7.3 metres long that have been caught in the past. This is still the figure that scientists quote as the maximum length of this relatively unknown denizen of the deep.

4.25 > Record-breaking fish: Greenland sharks live for hundreds of years.

development of many cold-blooded sea-dwellers in the polar regions takes five to ten times as long as that of thermophilic species in the mid-latitudes. The embryonic stage is often followed by slower growth and delayed sexual maturity. Thus while fish in warmer regions are usually ready to mate after one to four years, the larger fish species in the Antarctic take between six and ten years to reach this point. The Patagonian toothfish *(Dissostichus eleginoides)* does not reach sexual maturity until it is 13 to 17 years old. Some Antarctic ascidians, bryozoans and sponges form an exception to this rule: they are also cold-blooded, but various studies have found that they grow or spread relatively quickly. Nevertheless, even these animals develop more slowly than related species in the mid-latitudes.

The delayed development of polar species is partly attributable to the fact that cold hinders the animals' protein metabolism – i.e. the constant synthesis of proteins and their subsequent breakdown into amino acids in the cells. Continuous protein synthesis is an essential process in growing organisms, enabling protein to be transported to the organs and structural elements. At temperatures of zero degrees Celsius and below, however, it becomes difficult for cold-blooded creatures to maintain their protein metabolism and produce many fully functioning proteins. Researchers have discovered that in the cells of Antarctic species up to 80 per cent of the synthesized proteins are not re-used but are instead broken down again. In thermophilic species the corresponding figure is just 25 to 30 per cent. Polar species have a particularly high concentration of ubiquitin, a protein molecule that is responsible for identifying and removing damaged proteins. These faulty proteins are degraded in a particular part of the cell nucleus, the proteasome. In polar fish the ubiquitin is activated between two and five times more frequently than in fish from the mid-latitudes.

As a result of this and other cellular features, the protein metabolism of cold-blooded animals in the polar seas yields relatively few proteins that can ultimately be used for growth. This means that growing is a particularly energy-intensive process for polar species and in many of them it therefore proceeds very slowly. On the other hand, the cold-blooded inhabitants of the Arctic and Antarctic Oceans reach an unusually advanced age. Larger species of fish such as the Patagonian toothfish, which lives in the Antarctic, have a life span of between 15 and 30 years. The Antarctic bivalve *(Laternula elliptica)* lives for up to 36 years. The ocean quahog *(Arctica islandica)*, a species of clam found in the far north, is a record-holder: in 2006, British scientists found a specimen off the coast of Iceland that was 507 years old.

Researchers also attribute the slow growth of cold-blooded sea-dwellers to the extreme seasonal changes that affect the polar seas. Most cold-blooded animals only grow when they find food – but for many polar species sufficient quantities of food are available only during the periods of algal bloom that occur in summer. In the Antarctic, for example, more than 95 per cent of the species that feed on free-floating phytoplankton or algae growing on the sea floor stop eating in winter, while those that do continue to feed consume only a small percentage of what they would otherwise eat. One of the consequences of this is that the animals' growth is almost entirely limited to the summer.

Always in energy-saving mode

It is not only the development of cold-blooded creatures that proceeds slowly in the polar regions: their everyday lives are also spent in energy-saving mode. This means that they move particularly slowly and avoid unnecessary effort. For example, Antarctic fish do not chase after their prey in the water column but conserve their energy by lying in wait for them on the sea bottom. *Adamussium colbecki*, a bivalve found in the Antarctic, closes its valves only half as often as molluscs in warmer regions, and the predatory snail *Trophonella longstaffi* takes 28 days to bore through the shell of its prey and eat it – a task for which related species in water of ten to 15 degrees Celsius need just ten to twelve days.

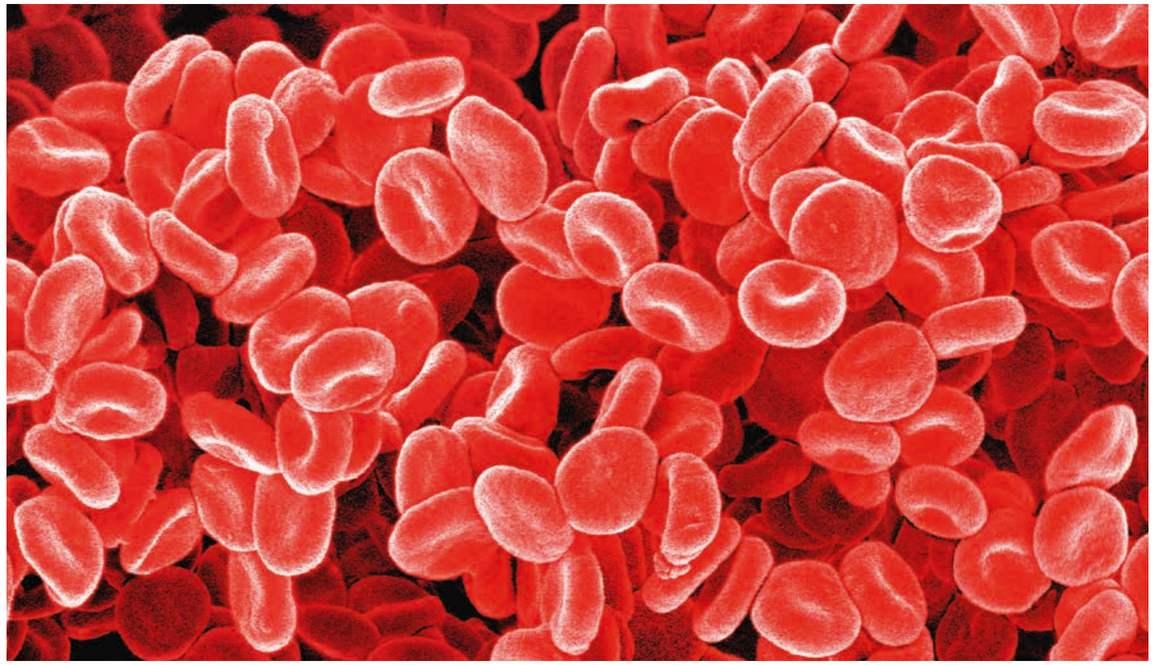
Naturalists currently know of only two adaptations developed by marine creatures in the Antarctic to make up for the disadvantages of the temperature-related effect on movement and enable them to operate at a speed akin to that of their non-polar cousins. The first involves the swimming speed of Antarctic fish. They have around twice as many mitochondria in their muscle cells as related species in warmer seas. This enables Antarctic perch to generate so much energy that they can when necessary swim just as fast as comparable species from the mid-latitudes. The second example is supplied by the Antarctic bivalve *Laternula elliptica*: because its foot muscle is two to three times the size of that of related molluscs in the mid-latitudes and tropics, it can dig itself into the sea floor just as fast as they can.

Fats, frost protection and colourless blood

The strategies for adapting to life in the polar seas with which people the world over are most familiar are those adopted by fish. All species of fish that live in waters of below zero degrees Celsius prevent themselves freezing to death by producing antifreeze substances in the form of glycoproteins. These are found in all the fishes' body fluids and they are not excreted by filtering organs such as the kidneys. Glycoproteins are sugar compounds that inhibit the growth of ice crystals in the fishes' tissues. As soon as an ice crystal starts to form, the glycoproteins accumulate in this miniature crystal and prevent further water molecules docking on to it. The tiny ice/sugar complex that arises is then excreted via the metabolism. Using this protective mechanism, the fish reduce the point at which their body fluids freeze to below minus 2.2 degrees Celsius and are able to survive ambient temperatures of up to minus 1.8 degrees Celsius. This is an adaptive strategy that fish from the Arctic and Antarctic have developed completely independently of each other; it remains one of the best examples anywhere in the world of parallel evolution – the development of identical characteristics in unrelated species.

A second distinctive adaptive strategy occurs only in the Antarctic Ocean. The Southern Ocean is home to the icefish or white-blooded fish (Channichthyidae), a family of Antarctic fish. Sixteen species of this family of predatory fish have no red blood corpuscles and they also lack haemoglobin, the red pigment that gives blood its colour. Their blood is completely translucent. Haemoglobin is

Radiocarbon dating
Radiocarbon dating, also known as C14 dating, is a method of determining the age of organic matter. Scientists calculate the relative quantities of the radioactive carbon isotope ^{14}C and the non-radioactive isotope ^{12}C in the sample; the resulting ratio indicates how many years have elapsed since the plant or animal died.



4.26 > Human red blood corpuscles are shaped like tiny biconcave discs and filled with the iron-rich blood pigment haemoglobin. Their shape enables them to transport oxygen very efficiently. The blood corpuscles also prevent the toxic haemoglobin escaping into the blood stream.

responsible for transporting oxygen in the bodies of many vertebrates, including humans. Each molecule of the pigment has four docking points for oxygen molecules; this is a particularly efficient method of transporting oxygen from the lungs, where it is taken in, to the parts of the body where it is needed. On the return journey the haemoglobin molecules pick up the carbon dioxide produced in the tissues and take it back to the lungs, where it is exhaled.

Excellent as this gas transport system is, haemoglobin is not entirely beneficial. Free haemoglobin in the body can be toxic: that is why it is encapsulated in the red blood corpuscles in humans and many vertebrates. In addition, haemoglobin becomes less efficient at binding oxygen as temperatures fall. Under very cold conditions, the presence of many red blood corpuscles carrying haemoglobin can make the blood more viscous and hence harder for the arteries to transport – especially when miniature ice crystals are also floating in the blood, as is the case in the Antarctic fish.

To prevent this problem, many species of polar fish have in the course of evolution reduced the number of red blood cells in their bodies. The icefish have even managed to do away with haemoglobin entirely. They live only from oxygen that diffuses directly into their blood in their enlarged gills or via their skin. The oxygen then dissolves physically in the blood, which means that the oxygen molecules do not dock on anywhere but are transported as they float freely in the blood.

However, the amount of oxygen dissolved in the blood in this way is fairly small. Icefish such as the blackfin icefish *(Chaenocephalus aceratus)* have to make do with a quantity of oxygen in their blood that is about ten per cent less than that available to red-blooded Antarctic fish. Researchers now think it likely that this haemoglobin-free oxygen supply in icefish only works because the cold conditions in the Antarctic Ocean mean that almost all the fish there have a metabolic rate ten to 25 times slower than that of fish in warm seas of 30 degree Celsius, with the result that the Antarctic fish use less oxygen. Furthermore, the cold water masses of the Southern Ocean are very oxygen-rich, with an oxygen concentration that is almost twice that of tropical seas, making it easier for all inhabitants of the Antarctic waters to take in oxygen. If fish outside the Antarctic had at some point stopped producing haemoglobin, they would have died immediately, but under Antarctic conditions such creatures still have a chance of survival.

Nevertheless, the fish with “white” blood display some specific characteristics that suggest that their circulatory systems must handle very large quantities of blood in order to provide a sufficient supply of oxygen. For example, by comparison with fish with red blood corpuscles, icefish have a heart so large that it pumps four to five times as much blood, arteries that are one-and-a-half times bigger in diameter and a blood volume two to four times greater.

The colder the habitat of cold-blooded sea-dwellers becomes, the more frequently they incorporate unsaturated fatty acids into their cell membranes. This enables the membranes to maintain their fluidity and hence remain fully functioning at low temperatures. Without this protective mechanism, the membranes would become gel-like in the cold and lose the permeability that is vital to survival.

Antarctic fish also have no swim bladder. So that they can nevertheless move with as little expenditure of energy as possible, they store lipids in their liver and other cells. These fats provide additional buoyancy. The fish also reduce their body weight by incorporating relatively little calcium into their skeleton and scales, replacing it where necessary with cartilage. As a result, the skeleton of the blackfin icefish appears almost transparent.

Polar giants

Although most of the cold-blooded inhabitants of the polar seas grow slowly, some of them – especially those in the Antarctic – reach a remarkable size. This has led researchers to coin the term “polar gigantism”. The sea spiders (Pycnogonidae) of the Antarctic are a good example: they achieve a diameter of more than 50 centimetres, while the largest sea spiders in moderate latitudes grow to no more than three centimetres across. The amphipods (flea crabs) of the Southern Ocean are up to nine times as long as their tropical cousins, and the cup-shaped glass sponges reach record sizes of two metres in height and 1.5 metres in diameter.

The blue blood of the Antarctic octopus

Haemoglobin is just one of four respiratory pigments used to transport oxygen in the animal world. Invertebrate organisms such as bristle worms use the green pigment chlorocruorin. Peanut worms (sipunculids), penis worms (priapulids) and brachiopods depend on a blood pigment called haemerythrin. When deoxygenated haemerythrin is colourless, but with oxygen on board it is a violet-pink colour. By contrast, molluscs, spiders, scorpions, crabs, lobsters and cephalopods (such as squids and octopuses) form the blue copper-based pigment haemocyanin. It is thought that in cold water that is low in oxygen, haemocyanin is a more efficient transporter of oxygen than haemoglobin. Nevertheless, at cold temperatures it is difficult for the oxygen in the tissues that has been taken in during respiration to separate from the blue pigment again.

The Antarctic octopus *Pareledone charcoti* has two ways of offsetting this temperature disadvantage. Firstly, its blood contains up to 46 per cent more haemocyanin than that of related octopuses that live in warmer water. Secondly, a lot of oxygen diffuses directly into the blood in the animal’s gills and dissolves physically there. By these means the little octopod that inhabits the shallow shelf waters of the Antarctic Peninsula ensures that even at temperatures as low as minus 1.9 degrees Celsius its body is supplied with sufficient oxygen right to the tips of its tentacles.

4.27 > The blood of the Antarctic octopus *Pareledone charcoti* contains up to 46 per cent more respiratory pigment than that of its warm-water counterparts.

The factors behind this gigantic polar growth have long been hotly debated by scientists. The reasons that have been put forward include:

- **Low maintenance costs:** Because temperatures in the Antarctic Ocean are low and the metabolic rate of most cold-blooded species is restricted, polar organisms generally need to expend less energy to maintain a large body than similar-sized animals in warmer regions.
- **High oxygen content of the polar seas:** This eases respiration and hence metabolism.
- **High concentration of silicon in the water:** This enables diatoms, glass sponges, radiolarians and other organisms to build up their silicon-based skeletons without expending excessive energy.
- **Abundant supply of food in summer:** The large algal blooms constitute a rich source of food that provides ideal growing conditions for animals with a slow metabolic rate and encourages growth-promoting competition between individuals.
- **Seasonal fluctuations:** In relation to their body mass, larger organisms need less energy than smaller ones. Bigger creatures can also lay down larger energy reserves, which puts then at an advantage at times when little or no biomass is being produced.

Throughout the Earth's history, competition between species has repeatedly led to extreme growth – the dinosaurs are just one example among many. However, the past also shows that these large species usually have difficulty adapting to changes in the environment. This is one of the reasons why scientists believe that global warming may have a greater impact on the giants of the polar seas than on smaller species.

Large eggs, attentive parents

Polar fish lay a relatively small number of eggs, but these eggs are considerably bigger than those of thermophilic species. In addition, Antarctic fish are often surprisingly active in caring for their young: they deposit their eggs on rocks on the sea floor or in the oscula of glass sponges and guard them until they hatch.

The flea crabs and krill of the Southern Ocean also produce strikingly large eggs that are usually two to five times as big as the eggs of related species in lower latitudes. The trend towards larger eggs in the polar regions is apparent even within a species. For example, the eggs laid by the Antarctic crustacean *Ceratoserolis trilobitoides* in the Weddell Sea are almost twice the size of those spawned by the same species in the vicinity of South Georgia a little further north. Scientists attribute this phenomenon partly to the uncertain availability of food in the polar regions. While animal species in warmer oceans can be fairly certain that their offspring will find sufficient food and grow quickly, this is not the case in the polar seas where food is sometimes hard to come by and the low temperatures make for long development times. For these reasons the young are usually given larger food reserves at the start – that is, in the egg. In addition, the offspring are usually somewhat larger when they hatch, thus increasing their chances of survival at the most critical stage of their lives. Scientists have also discovered that the cold-blooded creatures of the cold, oxygen-rich polar seas have larger cells than related species in warmer waters that contain less oxygen: this is another simple reason why their eggs are larger.

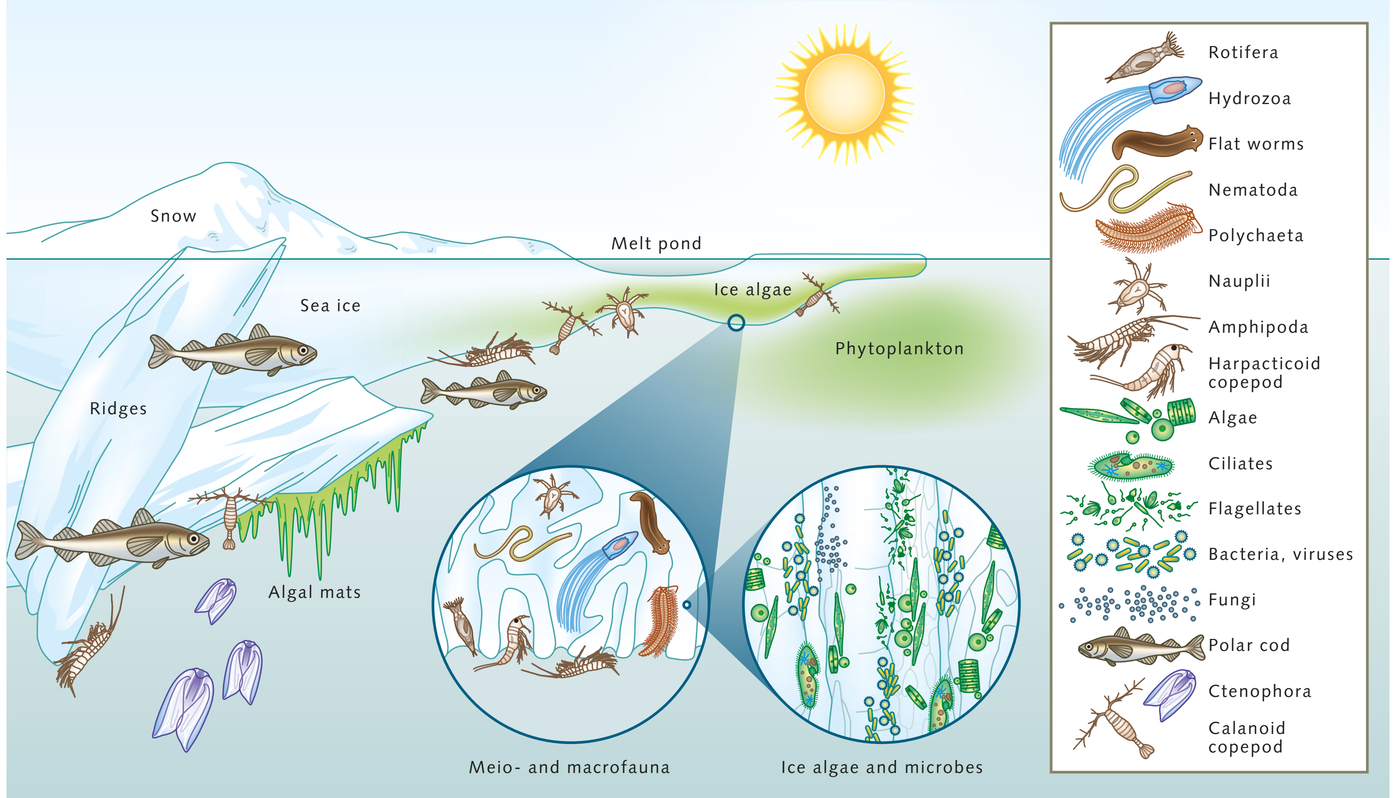
After spawning and fertilization, the life cycle of many polar species again differs from that of their thermophilic cousins. While invertebrate species in warmer regions often pass through a larval stage during which they must actively search for food (planktotrophic nutrition), the young of many Antarctic species are provided with a yolk sac that supplies the larvae with food to last them until they reach the next developmental stage in their metamorphosis; this is termed lecithotrophic nutrition. The main reason for this is once again the extended development time as a result of the cold conditions in the polar seas. The less food the larvae find, the more slowly their already protracted development proceeds; this in turn means that there is a longer period during which the young are at risk of being eaten themselves. The larvae of the Antarctic starfish *Odontaster validus*, however, must search for their own food and may spend up to 180 days in the water column before they settle on the sea floor and complete their metamorphosis to young starfish.

Life in, on and under the sea ice

The sea ice of the Arctic and Antarctic provides a unique habitat for the flora and fauna of the polar regions – even in those parts of the polar seas in which ice cover is present only at certain times of year. Scientists have identified more than 2000 species of algae and animals that live in or on sea ice – the majority of them too small to be seen with the naked eye. In addition to these species there are numerous bacteria, archaea, viruses and fungi that are adapted to the cold. In consequence, researchers now believe that the sea ice harbours a biological community made up of several thousand species, the growth and reproduction of which underpins the survival of all the marine fauna of the polar regions.

At the start of this important food chain are the ice algae: when the seawater freezes, many of these become encased in the ice together with particles, nutrients, a whole host of bacteria and all sorts of microorganisms. Unlike meat and vegetables in the domestic freezer, though, the organisms themselves do not freeze; instead they survive on the underside of the ice or in the vast number of small pockets and channels full of brine and seawater that form in the sea ice. To exist in this extremely salty environment at temperatures as low as minus ten degrees Celsius in the Arctic and minus 20 degrees Celsius in the Antarctic, the ice-adapted microorganisms have altered the composition of the lipids in their cell membranes. This prevents the membranes hardening and ensures that the organisms can continue to absorb nutrients from the seawater. Protein production in the cells is also adapted to the cold so that all the processes vital to survival proceed as smoothly as possible even at low temperatures. Ice algae also form antifreeze proteins and lay down fat reserves in summer that

4.28 > In spring and summer the many pores, pockets and brine channels of the Arctic and Antarctic Oceans support flourishing and species-rich communities of cold-adapted ice algae, bacteria, archaea, viruses, fungi and microorganisms. Scientists have identified more than 2000 species that live in or on sea ice.



enable them to survive the long winter. Despite these survival strategies it is nevertheless the case that the warmer and less salty the sea ice is, the better the sea-ice flora and fauna will flourish.

The ice-algae community consists mainly of diatoms, of which many different species occur in both polar regions. The number of ice algae present in a block of sea ice depends on how much light penetrates the ice, on its salt content and on the nutrients that are encased in the ice or available in the water beneath. Multi-year sea ice usually contains more species of algae than young ice. These relatively old floes also function as a sort of seed bank – especially in the pack ice, which frequently consists of newly formed ice, year-old ice and multi-year floes. In the spring, as temperatures rise and the ice becomes more porous, algae from the multi-year ice migrate to the younger ice and start an algal bloom there.

Ice algae flourish mainly in the lowest layer of the ice, close to the water. Species such as the Arctic diatom *Melosira arctica* also colonize the underside of the ice; in spring they sometimes form algal mats that trail downwards into the water column for up to two metres. Bacteria, on the other hand, are found in almost all layers of the sea ice, although they cluster in the lowest layer and on the ice surface.

The species community of the sea ice spends the long, dark winter in a relatively torpid state. But in the spring, when the sun once again climbs above the horizon, the algae in the lowest ice layer quickly grow and multiply, drawing the nutrients that they need from the seawater. As soon as the ice algae start to bloom, tiny algae eaters such as copepods, amphipods and krill larvae fall on the growing mountain of food. Some of the algal build-up sinks downwards and is devoured on the sea floor by sea cucumbers and other bottom-dwellers.

When the feasting starts in the many niches of the ice, the first zooplankton hunters are already lurking directly below the ice. In the Arctic these species include predatory flea crabs such as *Apherusa glacialis* and *Gammarus wilkitzkii*. But they also need to be careful, because alongside the flea crabs there will be polar cod and Greenland cod hunting for zooplankton under the ice. The fish mainly seek out amphipods and copepods, but they also eat mysids (opossum shrimps). The polar cod actually spawns in the labyrinth of the pack ice. Its millions of young spend the first year of their life concealed in the nooks and crannies of the ice. With the pack ice, they migrate from the spawning areas north of Siberia to the central Arctic. By diving under the ice, scientists have also discovered that jelly-like zooplankton such as comb jellyfish can occur in dense clusters under the ice. These animals seem to gather mainly in areas where the sea ice projects particularly deeply into the water column, thus causing upwelling and downwelling of the water.

Mammals and birds have two strategies for gaining access to the larder under the sea ice. They may use holes and cracks in the ice to break into the feeding grounds; this method of hunting is used in particular by various seal species of the Arctic and Antarctic Oceans. Alternatively, they may wait for the ice-free summer. This is the method adopted by Arctic mammals such as beluga whales and the big baleen whales. They spend the winter outside the sea-ice zone, not travelling north until the ice slowly retreats and large algal blooms form in the marginal ice zone.

Polar bears hunt seals on the surface of the sea ice, thus forming one of a number of end points in a food web the existence of which is directly linked to the sea ice. The life style of each member of this web is so precisely adapted to polar conditions that these species would have little chance of survival elsewhere. For all of them, the shrinking of the Arctic and Antarctic sea ice means a loss of vital habitat.

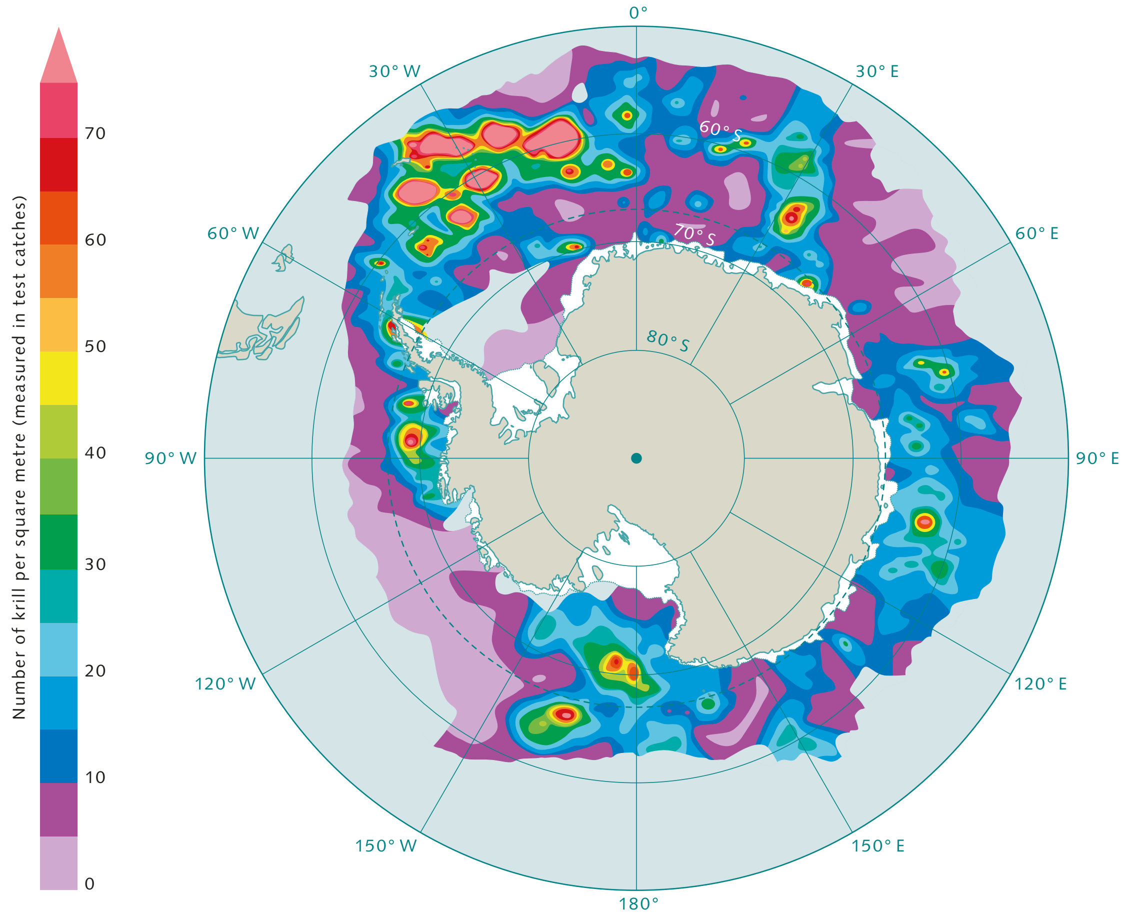
Antarctic krill – the mass phenomenon

A keystone species of the polar regions that depends directly on the sea ice for its survival is the Antarctic krill *(Euphausia superba)*. This bioluminescent crustacean, sometimes referred to as a light-shrimp, is a type of zooplankton that has garnered many superlatives. Its body length of up to six centimetres makes it one of the largest creatures of its type in the Southern Ocean. Individuals can live for up to eleven years and in terms of biomass they are one of the most abundant species on the planet. It is estimated that there are 133 million tonnes of Antarctic krill in the circumpolar regions, excluding larvae.

4.29 > Viewed from below, the Antarctic pack ice forms a rugged landscape in which algae colour the underside of the ice greenish brown in places where the most light penetrates.

Only humans weigh more in total. The term “krill” comes from the Norwegian word for whale food. It used to include other zooplankton species such as winged snails (Pteropoda) and jellyfish, but in everyday language the word is now used to refer only to *Euphausia superba.*

Antarctic krill occur only in the Southern Ocean and are thus one of the many endemic species of the Antarctic. There are five other species of crustacean in Antarctic waters, including *Euphausia crystallorophias*, the ice krill or crystal krill. This species lives mainly in the very cold marine shelf regions in the south, while *Euphausia superba* prefers deep sea areas further north with warmer average water temperatures of between zero and three degrees Celsius. The habitat of *Euphausia superba* is thus limited to somewhat more than half of the extent of the Southern Ocean – more precisely the area between 51 and 74 degrees south. Scientists have identified six large concentrations – one in the northern Weddell Sea and the Scotia Sea, one off Enderby Land, one around the Kerguelen Gyre, two smaller accumulations in the north of the Ross Sea and one population in the Bellingshausen Sea to the west of the Antarctic Peninsula. Because of this patchy distribution, the krill is not the link between primary producers and higher consumers in all parts of the Southern Ocean. Scientists have now identified three zooplankton communities in the Southern Ocean and their corresponding keystone species. The zooplankton in the northern part of the Antarctic Ocean are dominated by the salp *Salpa thompsoni* and the amphipod *Themisto gaudichaudii.* In the southern part, on the other hand, it is mainly the ice krill and the Antarctic silverfish *(Pleuragramma antarctica)* that occupy the key positions in the food web, with the Antarctic krill playing an important but nevertheless subordinate role. In the middle, however, the Antarctic krill and its close relative, the euphausid *Thysanoessa macrura*, plus a number of copepods, are the main prey of hunters such as fish, whales, seals, penguins and other seabirds.



4.30 > Using data from net catches and other sources, scientists have found that populations of Antarctic krill are distributed unevenly around the southern continent. Particularly large swarms occur in the northeast of the Antarctic Peninsula, off the coast of Enderby Land, around the Kerguelen Gyre, in the Ross Sea and in the Bellingshausen Sea.

In the regions where they flourish, the krill occur in swarms of up to 30,000 animals per cubic metre of water. In the Antarctic summer the krill swarms usually occupy the upper 50 to 150 metres of the water column. At the start of winter in April, however, they often sink to a depth of about 200 metres, but they have also been sighted at depths of 1000 to 3500 metres.

The eggs of the crustaceans, which the females lay from January to March, sink to a depth of more than 2000 metres. In the deep sea, free-swimming larvae emerge from the eggs; as the summer draws to a close the larvae rise higher and are carried by the surface currents in the upper part of the water column. Thus the krill larvae that hatched in the Bellingshausen Sea migrate within 140 to 160 days to the waters around South Georgia.

The young krill survive their first winter by hiding in the niches, hollows and cracks of the sea ice, feeding in autumn on the ice algae and in winter mainly on copepods and other microorganisms. Formation of the sea ice early in the winter appears to be an important factor, enabling the larvae to find protection and food for as long a period as possible. When the ice melts in spring, triggering the growth of algal blooms, the crustaceans complete the final stage of their development and become young adults.

The survival prospects of the mature krill are less heavily dependent on the sea ice. Some crustaceans survive the dark part of the year by ceasing to eat and reducing their metabolic rate by up to 50 per cent. During these fasting periods the animals may actually shrink. Other creatures look for alternative sources of food: they eat zooplankton that are still floating in the water column, or they sink to the sea floor, where they eat plant and animal remains that have trickled down. It is the length of the day that determines when the crustaceans’ metabolic rate and feeding behaviour switch to the winter pattern. This information is derived in part from laboratory studies which showed that under winter light conditions the animals ate very little, even if plenty of food was floating in the aquarium.

What lived under the Larsen A and B ice shelves?

In 2007, following the sudden collapse of the Antarctic ice shelves Larsen A (1995) and Larsen B (2002), scientists had a unique opportunity to study the animal life in the previously unexplored habitat beneath the great tongues of ice and to observe how the fauna was changing as a result of the loss of ice. Their survey showed that before the collapse of the ice shelves the ocean currents carried so little food beneath the ice tongues that only a few suspension eaters such as the vase sponges *Rossella nuda* and *Rossella racovitzae* were able to exist under the ice. They occurred so sporadically and were so small in size that the researchers thought each animal reminiscent of a solitary tennis ball lying on a tennis court with the next sponge, metaphorically speaking, not on the same court but on an adjacent one.

However, the biologists were surprised to find 16 animal species from the deep Antarctic sea under the ice shelves; most of these were echinoderms such as the sea lilies *Bathycrinus australis* and *Dumetocrinus antarcticus*. As a result of this discovery the scientists concluded that living conditions under the shelf ice probably resembled those in the deep sea and it was this that had enabled the dwellers of the deep to migrate to the shelf-sea zone.

The collapse of the ice altered the supply of light and food in the water. Although the areas were and still are frequently covered by sea ice, algal blooms occurred from time to time. Other organic material was carried in by the currents, enabling pioneer species such as sea squirts and glass sponges to colonize the deserted areas. The vase sponges successfully reproduced and, attracted by the food supply, ice krill, Antarctic krill and Antarctic silverfish swam in the water column. This in turn drew in larger hunters. In the summer of 2007 the biologists found that there were roughly as many crabeater seals and dwarf whales in the former shelf-ice region as would normally occur elsewhere in the Weddell Sea or off the west coast of the Antarctic Peninsula. In other words, the fauna of the Weddell Sea was already reconquering the habitat that had been lost for so long.

Polar ecosystems in retreat

> Global warming is changing the foundations of life in the polar regions – in water and on land. With the diminishing sea ice, the prime food store of the polar seas is shrinking. Rising temperatures are forcing the cold-loving species to take flight, but scarcely any refuges are left. Their territories are being invaded by species from the middle latitudes. Over time, these changes will lead to the disappearance of the unique polar flora and fauna. The first signs of this are already apparent.

Altered environmental conditions due to climate change

Climate change is transforming biological communities throughout the world, but most dramatically in the polar regions. In recent decades, the Arctic and regions along the Antarctic Peninsula have warmed so much that the vital physical determinants of life have changed significantly. For the biological communities in the ocean these include:

- water temperature,
- ocean currents,
- salt and nutrient content of the water,
- carbon dioxide content of the water (ocean acidification),
- oxygen content of the water,
- volume of sea ice, and
- the frequency of iceberg calving.

For the biological communities on land, climate change has had an impact on the following:

- air temperature,
- type and amounts of precipitation,
- duration and extent of snow and ice cover,
- extent of permafrost,
- frequency and intensity of extreme weather events such as heat waves, and
- the amount of coastal erosion.

For the coming decades, climate researchers predict that the polar regions will continue to be subjected to the effects of rising temperatures, increasing acidity of sea water, intensified melting of snow and ice, changing precipitation levels, rising sea level, and large-scale thawing of permafrost soils.

Two types of adaptation

Organisms react to changes in their environment initially by trying to adapt their behaviour to the new conditions within a short time (acclimatization). Depending on their baseline situation, they may accelerate respiration and metabolism, pump more blood or water and nutrients through the body, perhaps eat more or, if they are mobile, migrate to areas where more familiar environmental conditions prevail. But these attempts at adaptation usually require an output of additional energy that the organisms have to generate. If they can do that, they have a relatively good chance of survival. But if they lack the necessary reserves, individuals may quickly reach their physical limits and be at risk of dying.

However, those individuals who succeed in acclimatizing in the short or medium term usually also reach the age necessary for sexual reproduction and, under optimal conditions, have the chance to adapt genetically over a number of generations. The organisms may produce offspring whose genetic make-up is favourably modified such that the new generation can cope better with the altered living conditions than the parent generation (genetic adaptation).

Both of these options are available to the flora and fauna of the polar regions. For two reasons, however, they represent a major, if not overwhelming challenge. In order to survive in the Arctic and Antarctic regions, most polar animals and plants have already reduced their metabolism and energy consumption so drastically at some time in the past that few of them possess sufficiently large reserves to compensate for the expected temperature increases in the long run. Furthermore, the slow evolutionary processes of many polar marine organisms preclude rapid generational changes. So the possibilities for adapting genetically to the new living conditions in a timely manner are very limited, especially for the more highly developed animals and plants. The outlook is different for organisms with short reproductive cycles. Bacteria, viruses and single-celled algae, for example, reproduce so rapidly that their prospects of genetic adaptation are much better than they are for clams, mussels, fish, birds or mammals. Individual adaptive capacity is therefore not as critical for microorganisms as it is for organisms with longer lifespans.

Ecosystems under pressure

Because the Arctic and some parts of the Antarctic are warming twice as fast as the rest of the world, the highly specialized biological communities in these two regions are under particular pressure. The many species-specific changes that researchers are now observing are represented by the following trends:

- In the two polar regions, depletion of sea ice is reducing the size of the habitat for species that use the ice as food source, resting area or nursery ground. Particularly in the Arctic, this means that feeding grounds are shifting poleward with the retreating ice margin. Birds and mammals here that have hunted or fished on the edge of the ice now have to travel greater distances.
- The spectrum of prey for polar predators is changing in the wake of ocean warming.
- The health and fitness of many animals are deteriorating due to food shortages.
- The decline in sea ice and the rising water temperatures are forcing polar sea dwellers to migrate to the few remaining colder regions. Such migrations will be much easier for mobile deep-sea species than for shelf-sea inhabitants that are adapted to life in shallow water.
- The rising air and water temperatures in the Arctic and Antarctic are paving the way to the polar regions for immigrants from the mid-latitudes. These newcomers may then compete with the native species for food. Or they themselves could become a less nutritious prey than the polar species that they replaced in the food web.
- Climate change affects polar biological communities in many ways due to its interactive processes. Various stress factors can either amplify or diminish each other’s effects.
- Exactly how climate-induced changes alter the lives of animals and plants in the polar regions depends to a large extent on regional conditions. The course as well as the degree of change can thus vary greatly from region to region.

Sea-ice retreat – the pantry is shrinking

The retreat of Arctic and Antarctic sea ice is already having a fundamental impact on biological communities, and on the individual species that depend directly or indirectly on the sea ice in any way. The thinner the ice is, the more

4.31 > Body of a dead grey whale north of San Francisco. It is one of more than 200 whale corpses that have been found on the west coast of the USA, Canada and Mexico since the beginning of the year.

4.32 > The winter sea ice in the Bering Sea is steadily retreating. At the end of the winter of 2018 it covered the smallest area of sea since the beginning of satellite measurements. Researchers believe that the causes include increasing air temperatures due to the meandering jet stream, combined with warmer water temperatures.

light is able to reach the ice algae in the spring, and the earlier the important algal blooms begin. Researchers believe that thinner sea ice in the Arctic that also melts earlier will initially boost primary production because the algae in the ice and in the water column will be exposed to more light through the course of the year. But there are two important requirements for increased algal growth. First, the ice and seawater must contain sufficient nutrients. The second requirement is that the amount of snow on the sea ice must not increase. A thick snow cover would prevent sunlight from penetrating through to the ice algae. A more stable stratification of the upper water masses could also inhibit their growth. When sea ice melts, the freshwater content of the upper water layer increases. As a consequence, the low-salinity surface water does not mix as readily with the denser, heavier, more saline and nutrient-rich deep water.

Computer simulations of sea-ice development in the Arctic region indicate that future ice-algae blooms will begin much earlier in the year. This temporal shift, in turn, threatens the survival of copepods as well as many other species of zooplankton whose life cycles have always been closely synchronized with the reproductive cycle of the ice algae. Scientists have been observing a decline in ice-associated amphipods around Svalbard, for example, since the 1980s. Premature ice-algae blooms, or even their complete absence, could initiate a fatal chain reaction such as the one recently observed in the northern Pacific Ocean.

In the past, ice algae have accounted for 60 per cent of the primary production in this region. But in the winter of 2017/2018, the area of sea ice around Alaska attained a size of just half of what was there in 1978. Accordingly, the subsequent ice-algae bloom in that year was also small. As a result, the zooplankton that feed on the ice algae starved first. The next victims were probably the fish species living under the ice, because the following summer the inhabitants of Alaska observed an abnormal number of seabird deaths. Large numbers of the common murre *(Uria aalge)*, which preferentially preys on ice-associated fish such as polar cod *(Boreogadus saida)* and capelin *(Mallotus villosus)*, starved to death. Just a few months later, by August 2019, the bodies of more than 200 starved grey whales had washed onto the west coast of North America. The animals presumably died because they could not find enough food during the previous summer in their Arctic feeding grounds in the Bering Sea and in the Chukchi and Beaufort Seas. Grey whales are the only baleen whales that search for food on the seabed. They filter amphipods, worms, mussels, fish eggs and other bottom dwellers out of the mud, and accumulate an abundance of fat reserves in the Arctic before migrating to the Gulf of California for the birth of their calves.

The ice-related collapse of fish stocks in the Pacific sector of the Arctic Ocean also had an impact on Alaskan fishermen. In the past, they had caught economically important species such as Alaska pollock *(Gadus chalcogrammus)* and Pacific cod *(Gadus macrocephalus)* in the Bering Sea. These species both prefer cold water masses, like those that previously formed a kind of cold-water pool in the Bering Sea. But in 2018 this pool was smaller than it had ever been before, presumably due to the absence of winter sea ice. At any rate, the schools of fish followed the cold water northward and out of the reach of the fishermen. If this chain of events is repeated in the coming years, the continued survival of the lucrative fishing industry in the Bering Sea will be seriously threatened. In 2017 the fishermen still caught and processed Alaska Pollock with a value of 1.3 billion US dollars. However, if the stocks permanently migrate to the north, the operation of the large industrial ships will no longer be profitable.

With regard to the continuing decline of sea ice in the Bering Sea, researchers are talking about an imminent regime change. By this, they mean the transformation of a polar marine ecosystem once focused on sea ice as the central component of the habitat and food supply, into a more temperate system, in which sea ice and its associated species play virtually no role.

4.33 > Because there is no longer sufficient summer sea ice off the Arctic coasts of Alaska and Russia, around 100,000 Pacific walruses have come to a beach on the Chukchi Sea to rest from their hunting excursions and give birth to their young. These mass gatherings have also taken place in the past, but as the sea ice recedes further, they are occurring more frequently.

Too little ice for walruses and polar bears

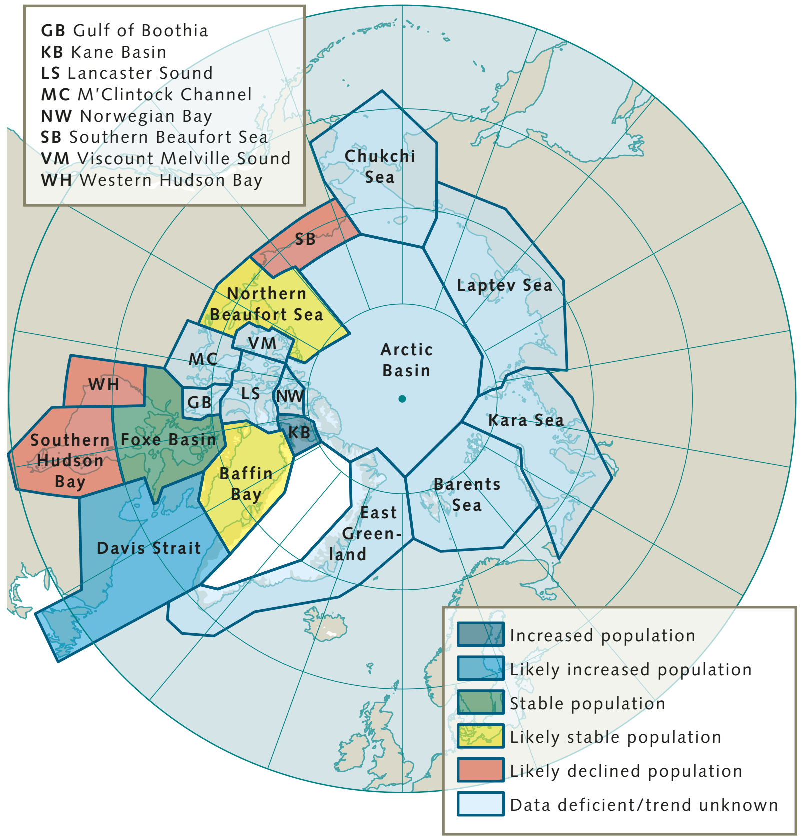
The retreat of sea ice in the Bering Sea is also altering the living conditions for the Pacific walrus *(Odobenus rosmarus divergens)*. Up to 3.6 metres long and weighing as much as 1900 kilograms, the walruses search for food on the sea floor of the Bering and Chukchi Seas, and in the past they would sleep in small groups on ice floes floating near their fishing grounds. The cows also delivered their calves on the ice and raised them there. But since 2007, researchers have been observing that the walruses are now much more rarely finding ice floes to use as resting platforms. Instead, the animals are forced to make their way back to the land. They often come by the thousands to coastal areas sheltered from the wind and waves. Exhausted and densely packed, they lie on the beaches in groups of up to 100,000 individuals. If the walruses are disturbed in this kind of situation, either by polar bears, airplanes or people, a state of mass panic can result. The heavy animals take flight blindly into the sea, ploughing through any individuals that are not able to get out of the way in time. Many of the calves do not survive this kind of mass panic.

Such stampedes, however, are not the only consequence of climate change for these large pinnipeds. With the increasing water temperatures in the Pacific sector of the Arctic Ocean, the food supply for the walruses is also undergoing changes. Subarctic bottom dwellers and po-tential prey animals like the graceful decorator crab *(Oregonia gracilis)* are migrating from the south into the Chukchi Sea, and are invading new habitats. Furthermore, the distances from the coast to the ice edge are becoming steadily greater for the animals. Native inhabitants of Alaska report that they are increasingly finding deep-sea fish in the stomachs of the walruses they hunt and significantly fewer mussels – an observation that indicates that the spectrum of prey for the large mammals is changing. What impacts these changes will have on the population as a whole remains to be seen. In the case of harp seals and hooded seals on the Atlantic side of the Arctic Ocean, researchers are already recording a decline in the birth rate, diminishing overall health, and dwindling populations. Scientists attribute these developments similarly to the decline of sea ice.

The outlook for polar bears is also discouraging. With the disappearance of sea ice, climate change is destroying the only habitat on which they can find sufficient food. Recent findings indicate that the bears require 60 per cent more energy than was previously thought. Even on days when the animals hardly move, they still burn more than 12,000 calories. This basic requirement can only be met by preying on ringed seals *(Pusa hispida)* and bearded seals *(Erignathus barbatus)*, which the bears hunt on the sea ice. Any other food source would not be sufficient to ensure the survival of the bears. In recent years, young polar bears in particular have been observed searching for alternative food sources on land. These animals were eating berries and kelp, chasing ducks and small mammals, and raiding the nests of snow geese *(Chen caerulescens)* and thick-billed murres *(Uria lomvia)*.

Scientists therefore assume that, in the long run, the unchecked decline of Arctic sea ice will lead to extinction for the polar bears. The hunt for seals can only be successful on the ice, where they initially prey on young animals in the late spring. These are still unable to escape into the water at this time, and as prey they have a fat content of 50 per cent. Then, when the new generation of seals are able to take refuge in the sea, the bears wait to ambush them at one of their many breathing holes.

Polar bears that have year-round access to the ice can hunt for seals at any time. Animals that live in regions where the sea ice melts extensively in summer have to spend the ice-free time on land and must fast most of the time. The longer these bears are unable to hunt at sea, the greater the danger of starvation becomes. In computer models, biologists have calculated mortality rates for adult bears in the western Hudson Bay. These indicate that three to six per cent of all adult males will die when the summer fasting period lasts 120 days. If the period is extended by 60 days, to a total of 180, 28 to 48 per cent of the bears will be threatened by starvation. Extended periods of fasting have also been shown to disrupt the reproductive capacity of these carnivores. In years when there is little sea ice, female polar bears give birth to fewer and smaller cubs, and mortality rates for the offspring increase.



4.34 > The Arctic polar bears are divided into 19 geographic groups whose population numbers are insufficiently known to researchers. In 2019, reliable data was available from only eight regions.

4.35 > A hungry polar bear preys on a colony of breeding seabirds on Coburg Island in Nunavut, Canada.

4.36 > As long as the absence of sea ice deprives the polar bears of access to the seal hunting grounds, they will search for food on land, for example in the garbage dumps of Arctic communities.

The decrease in average sea-ice thickness is a further factor causing problems for the polar bears, because thinner ice floes drift faster. The increased drift speed means that they will have to make a greater effort to continue hunting in their traditional territory. The greater effort, in turn, means an increased energy demand that the animals will have to meet. This is a challenge that is driving the bears increasingly closer to human settlements, or into regions where they have rarely been seen before. In June 2018, for example, a polar bear visited Summit Camp, a US research facility on the Greenland ice sheet. The station lies at an elevation of 3200 metres, and is located more than 400 kilometres from the nearest coast.

Estimates say that there are around 25,000 polar bears in the Arctic today, comprising 19 different populations. Information on developmental patterns is available for eight of these populations. Only in the Kane Basin southeastern of Ellesmere Island is the number of bears known to have increased. Scientists suspect that the case is similar for the population in the Davis Strait. So far, the populations in Baffin Bay, the Foxe Basin (Canadian Arctic Archipelago) and the northern Beaufort Sea appear to have remained stable. Conversely, the researchers are reporting declines in the southern Beaufort Sea as well as in the southern and western regions of Hudson Bay. If the scientific predictions are correct, polar bears will die out in these two regions within the next 30 to 40 years. During the same period, the total number of polar bears in the Arctic is expected to plummet by two thirds.

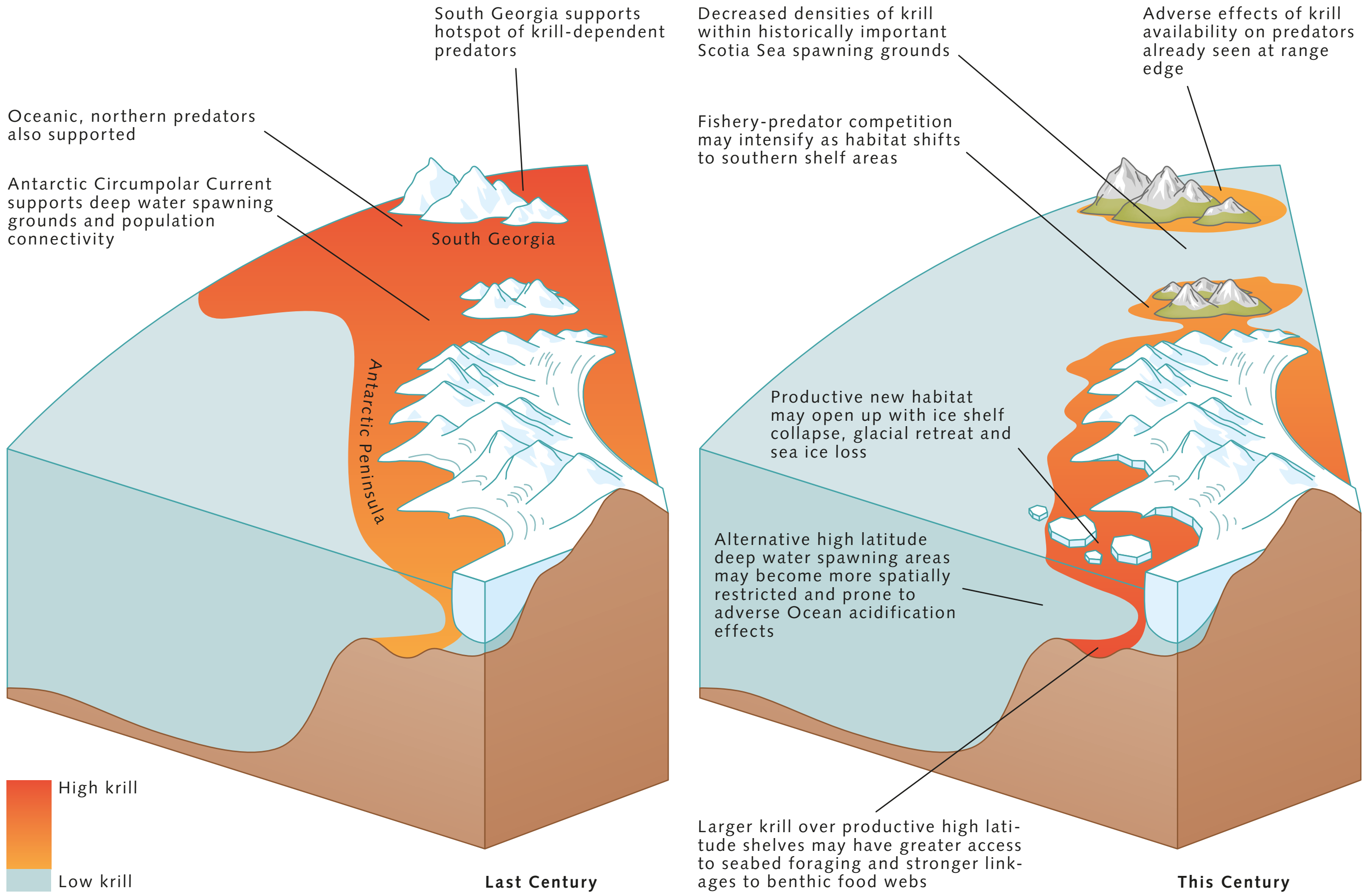
Not enough ice in the krill nursery

In the Antarctic, shrinking of the sea-ice cover has so far been occurring primarily on the western side of the Antarctic Peninsula, which is the nursery area for the krill population of the southwest Atlantic sector of the Southern Ocean (20° to 80° West). This community accounts for more than half of the total population, and is thus the largest concentration of krill in the Antarctic region. Scientists have analysed catch and size data for the krill over the past 90 years and found evidence of very fundamental change. Not only has the total number of krill decreased by more than 50 per cent, the large swarms today are located much further to the south than they were in the 1920s. At that time, the largest summer occurrences were around South Georgia. Now, however, these crustaceans live mainly along the northern and western coasts of the Antarctic Peninsula. Furthermore, the individual animals today are an average of six milli-metres longer than they were in the 1970s. This observation implies a demographic change within the krill swarms. The populations are now much older than they were earlier, which means that the Antarctic krill are producing fewer offspring, or that fewer of the offspring survive the larval stage.

The primary reason for this is presumed to be the retreat of sea ice on the western side of the Antarctic Peninsula. When ice is scarce the algal blooms are smaller, and the zooplankton species such as krill cannot find enough food in the springtime at the beginning of their reproductive cycle. A deficient food supply in the spring affects egg production and the hatching success of the offspring. In the past, the krill larvae and juvenile animals have been able to hide in the winter from predators, like the Antarctic silverfish, in the cavities, cracks and niches of the sea ice. Without this refuge, however, the crustaceans are at the mercy of their hunters.

Furthermore, the krill, also known as "light-shrimp", encounter altered living conditions in many fjords along the Antarctic Peninsula. Where glaciers have retreated onto the land, meltwater streams wash large quantities of sediment into the fjords and create turbidity in their waters. This pollution impacts krill in two ways. First, turbid water means less light for the various kinds of algae that live in the water column. These are no longer able to carry out a sufficient level of photosynthesis and thus grow much more slowly or die within a short time, and are no longer available as food for the krill. Second, when ingesting food, krill cannot actually distinguish between phytoplankton and sand particles. They consume whatever they filter out of the water. If their food consists mainly of sand grains, the light-shrimp starve. For this reason, the Antarctic krill has already disappeared from Potter Cove, an intensively researched glacial bay on King George Island. Its place in the food web has been taken over by salps, which can cope much better with the murky fjord waters.

The changes in the krill population in the southwest Atlantic sector have clearly left a mark on the species structure of the Southern Ocean. For example, the seals of South Georgia now give birth to calves that



4.37 > Warming of the Southern Ocean has led to the migration of Antarctic krill from their former territorial waters around South Georgia. They are now found further to the south in the coastal waters of the Antarctic Peninsula. The food webs in both areas have been permanently altered as a result.

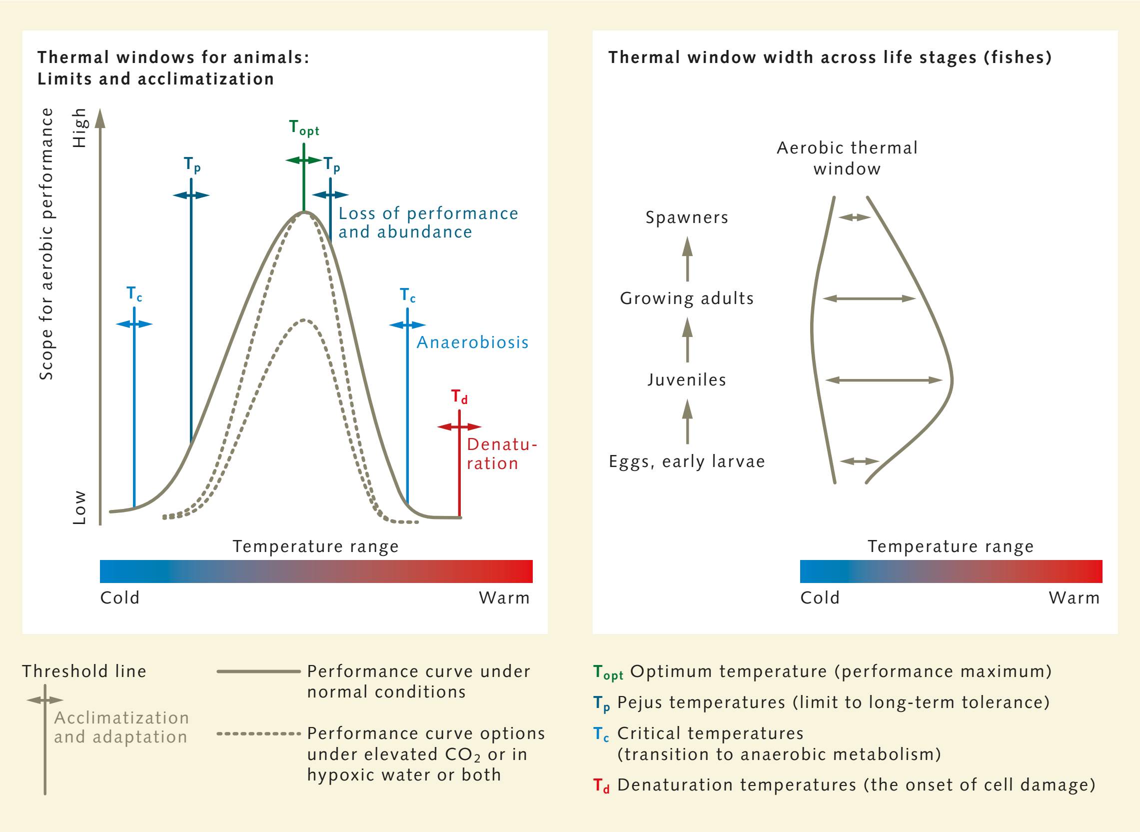
are much lighter than they were when the krill swarms were still abundant around the island. The southward migration of krill swarms is also making it difficult for Adélie penguins on the South Shetland Islands and along the west coast of the Antarctic Peninsula to find food. In recent decades their colonies have shrunk by as much as 50 per cent, although the declining krill population is not the only reason for this. Changes in the weather conditions on the Antarctic Peninsula have also played an important role.

Adélie penguins nest on snow-free and ice-free ground. If the breeding birds are caught off guard by rain or heavy melting of snow, their nests may be flooded and eggs or chicks lost. In the past, such losses have contributed to a decrease in the number of Adélie penguins along the Antarctic Peninsula, as have the diminishing krill population and the decline of the ice-associated Antarctic silverfish, another favourite food of the penguins.

Life at the thermal limit

In recent years, using a wide variety of methods, scientists have been studying how marine organisms respond to rising temperatures. Most of the laboratory studies indicate that cold-loving, ectothermic organisms native to the northern and southern polar seas are much less able to survive a period in warmer water than related species from temperate marine areas. Antarctic invertebrates like the bivalve *Limopsis marionensis*, the brittle star *Ophionotus victoriae*, and the brachiopod *Liothyrella uva* died at water temperatures of only three to four degrees Celsius. This places them among the most heat-sensitive marine organisms in the world.

In order to evaluate the adaptability of an ectothermic marine dweller, scientists determine the size of its thermal window. This refers to the range between the upper and lower temperature limits at which the organism can function smoothly. The width of this window varies depending on the species and the habitat. Animals from more temperate latitudes like the North Sea generally have a wider thermal window. This is necessary because they live in a marine region where the water temperatures vary greatly with the tides and seasons. This means that the animals have to endure the warm temperatures of summer as well as the cold winter conditions. The thermal windows of organisms in the tropics or polar regions, on the other hand, are two to four times smaller than those of the North Sea dwellers.



4.38 > Every organism has a limited temperature range within which it can function and exist. Researchers refer to this range as the thermal window. An organism performs most effectively when the ambient temperature is near the midpoint of its temperature window. If it gets warmer or colder, the functionality of the organism diminishes, even to the point of death. For most organisms, the size of the thermal window changes with increasing age. Fish, for example, can usually tolerate greater temperature fluctuations as young animals than they could in the embryonic stage.

The temperature limits for a particular species also vary with the age of the individual animal. It has long been assumed that larvae or juvenile animals have the smallest thermal window. It is often stated that a species cannot colonize in places where it gets too warm for them. This statement is true for the Atlantic cod and polar cod, among others. For these two species, a slight increase in water temperature is enough to kill a large proportion of their eggs. Research on a variety of invertebrate animal species from the Southern Ocean, however, indicates that their offspring react very differently to heat. In some studies, the mortality rates of juvenile animals did not increase until the temperature reached a level that was also dangerous for the adult animals. In others, the young animals were even more resistant to heat than the mature generations.

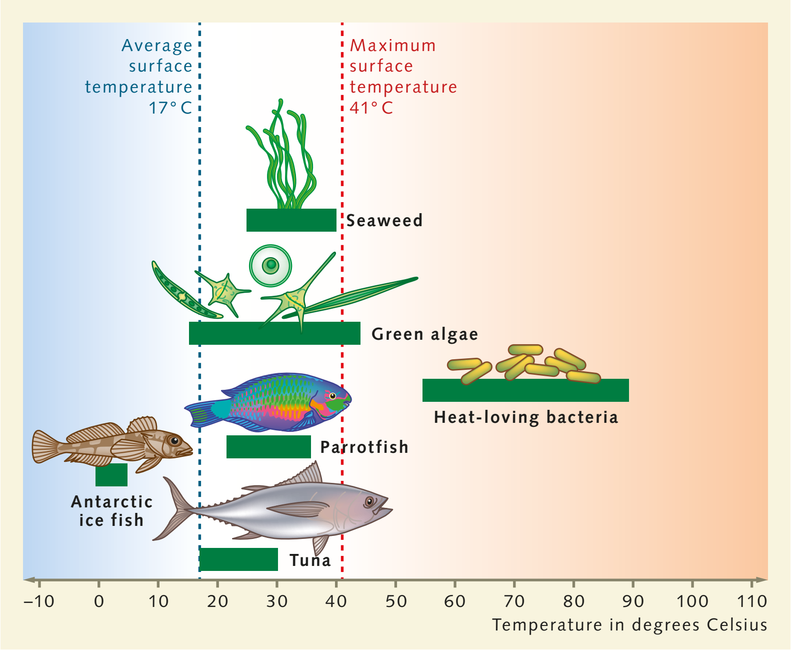
But it was also revealed that the offspring of polar species develop more rapidly in warmer water. If, for example, the Antarctic sea urchin *Sterechinus neumayeri* reproduces in water that is 0.5 degrees Celsius warm, the larvae sink to the seabed within 90 days after egg fertilization, where they then metamorphose into young sea urchins. In colder water, at minus two degrees Celsius, the animals require 120 days for this process, whereby the larvae also have more time to drift with the current to more distant regions. If the duration of the larval stage is shortened, there could be ramifications for the lateral distribution of the species.

4.39 > The embryos of the Atlantic cod require water temperatures of three to seven degrees Celsius in order to develop optimally. The eggs, about 1.5 millimetres in diameter, will die if the water is only slightly warmer.

There is now a basic assumption that most ectothermic animals in the polar regions would be able to survive over the long term in water that is as much as three to four degrees warmer. But if the warming exceeds this upper value, it would cause an increase in mortality and a greater number of deformities in juvenile animals. Another result would be that, for various reasons, the organisms would no longer be able to meet the increasing energy and oxygen demands that accompany rising water temperatures. When the water becomes warmer, all of the natural body processes of ectothermic marine organisms progress faster and therefore require more energy. Among other things, the animals digest the food they consume more rapidly, and a larger proportion of the energy they take in is used for their basal metabolism – the maintenance of basic normal body functions. If the animals ingest the same amount of food under these conditions as they did previously, they end up with less energy reserves for growth and reproduction than they had under colder conditions.

These and similar interactions are particularly threatening during the winter, when there is virtually no primary production in the polar seas due to the paucity of light. In the past, most cold-loving species have simply lowered their metabolism in winter. However, if global warming of the oceans continues, the energy demands will also increase during the polar night when food is scarce. The only individuals that will survive are those who are able to build up sufficient reserves.

From long-term studies on fish and other ectothermic organisms in the Antarctic region, it is also known that these species require a relatively long time to adapt to new



4.40 > Over generations, ocean dwellers have adapted to the conditions in their native waters, and have developed a corresponding range of temperature tolerance. The range is generally larger for species from the middle latitudes (tuna) than for species in the tropics or polar seas. Tropical and polar organisms commonly live at the upper or lower limits of their comfort zone.

environmental conditions. In laboratory experiments, up to nine months passed before the animals were able to restructure the fatty acids in their cell membranes to match the adjusted temperatures. This delayed acclimatization weakens the animals over the long term, because it means that many of the processes in their bodies do not function optimally for several months if the external conditions change quickly, as with a change of season, for example. Researchers are assuming that the water temperatures in the Antarctic will continue to fall to near the freezing point for the next one hundred winters. But they also believe that the winters will become shorter and the summers warmer. The cold-loving ocean dwellers will therefore be in a constant state of adaptation and will only rarely experience optimal conditions in the future.

Migration towards the pole

The easiest way for organisms to adapt to global warming is presumably to migrate to areas where familiar temperatures still prevail. For organisms living on land, this would be either the high mountain areas or regions further to the north or south. Sea dwellers, on the other hand, can migrate to greater depths or toward the poles. Researchers have been observing these temperature-induced migrations in plankton, invertebrates, fish and seabirds for decades, including in the peripheral areas of the polar oceans. Phytoplankton in the North Atlantic, for example, have been shifting poleward since the 1950s by a few hundred kilometres per decade. In the Southern Ocean, calcareous algae are found much further south today than they were 20 years ago.

Since the beginning of industrialization, the zooplankton populations of the world’s oceans have migrated an average of 600 kilometres towards the poles to evade rising water temperatures. In regions that have become particularly warm, the ranges of microorganisms have shifted by as much as 2550 kilometres.

The Atlantic cod *(Gadus morhua)* has already advanced so far to the north in its flight from the heat that it can now be found in large numbers in the waters around Svalbard in the summer. The warm Atlantic water masses overlie cold Arctic waters from the Barents Sea at this time of year, so the cod finds optimal conditions with water temperatures of around four degrees Celsius. Its Arctic relative, the polar cod *(Boreogadus saida)*, on the other hand, has to flee this temperature. As a cold-loving species it prefers water temperatures around zero degrees Celsius. The Intergovernmental Panel on Climate Change predicts that these and other cold-adapted inhabitants of the northern and southern polar seas will see their habitats continue to shrink because there are no other areas of refuge for them in the long run.

When immigrants from the middle latitudes advance into the polar regions, they may have to compete with established species for food resources. For example, Atlantic and Pacific killer whale populations are now also hunting seals in Arctic waters, and are thus competing with polar bears. Because of the northward migration of the Atlantic cod, the polar cod is confronted with a further competitor for food. Where these two fish species share the sea, they may hunt the same prey.

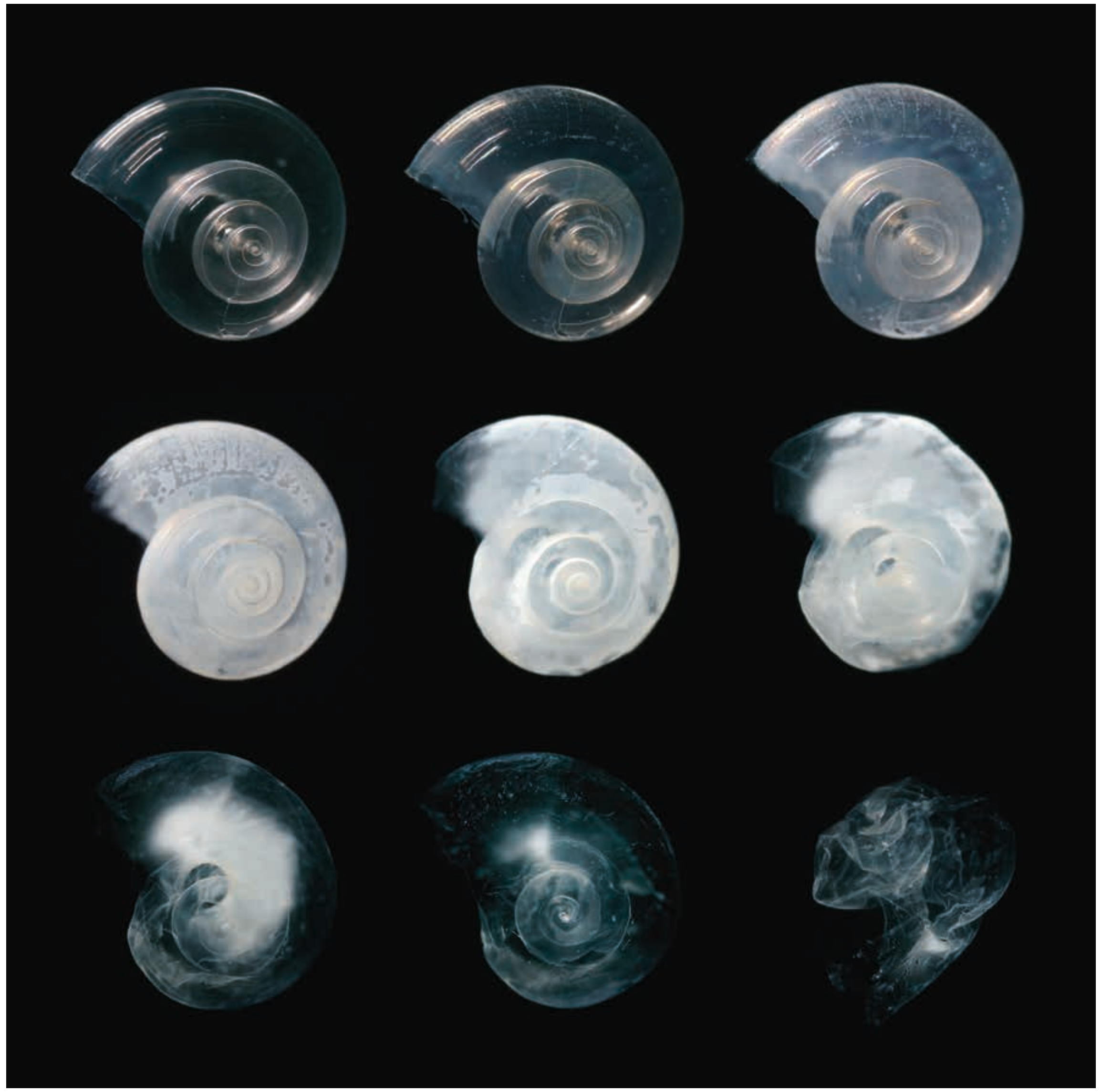
Immigrating species also change the food structure of the polar regions by becoming prey themselves while being significantly smaller and less nutritious than the

4.41 > Calcareous algae and other phytoplankton bloom in the spring and summer in the nutrient-rich waters of the Barents Sea, colouring this Arctic marginal sea bright green to milky blue. Researchers are noting that the magnitude of this algal bloom is increasing in the wake of climate change. At the same time, the blooms are occurring further to the north than they did at the beginning of the 21st century. This is due to the retreat of the Arctic sea ice.

native species they have displaced. One example of this is the Atlantic copepod *Calanus finmarchicus*. It is advancing into the Arctic Ocean via the North Atlantic Current, and in its northern range is now replacing more fat-rich Arctic species such as *Calanus glacialis* and *Calanus hyperboreus*. For the predators of copepods, this species substitution means that they have to consume larger volumes of the newcomers in order to obtain the usual amount of energy. Scientists are observing very similar patterns in amphipods.

The polar seas are acidifying

By acting as a gigantic carbon sink, the oceans have absorbed around a third of the carbon dioxide that human activities have released into the atmosphere since the beginning of industrialization. Thus the world's seas have slowed global warming. However, this absorption also leaves traces, because when carbon dioxide from the atmosphere dissolves in seawater, a profound chemical change occurs in the surface water. Seawater normally has an average pH value of 8.2 and is therefore slightly alkaline. This is because of the mineral components in the water, calcium carbonates such as calcite and aragonite, which were at one time dissolved from weathered stone on land and then washed into the sea.



4.42 > Researchers set up a laboratory experiment in which they kept the Antarctic pteropod *Limacina helicina antarctica* under the acidified conditions predicted for the year 2100 – assuming that humans do not cut their carbon emissions. The finding: the sea snail's calcareous shell dissolved within 45 days.

If the oceans absorb carbon dioxide, however, this gas, unlike oxygen, does not simply dissolve in water. On the contrary – a proportion of the carbon dioxide binds with the water, so that carbonic acid is produced. Anyone who makes their own sparkling water at home in a Sodastream understands this principle. When the button is pressed, carbon dioxide is injected into a bottle of tap water and immediately produces in it the bubbles typical of carbonic acid. To a certain extent, the same thing happens in the sea, but the carbonic acid in the sea is not stable: it breaks down into bicarbonates, the carbonic acid salts, and protons (hydrogen ions). The latter increase the acidity of the water and the ocean becomes more acidic.

The measure for the concentration of hydrogen ions in a solution is known as the pH value. However, this numerical value shows the concentration as a negative common logarithm. That means that the more hydrogen ions there are in a solution, the lower the pH value is. Since 1860 the mean pH value of the ocean surface has fallen from 8.2 to 8.1. This apparently small gradation on the logarithmic pH scale corresponds to an actual rise in acidity of 26 per cent – a change that the world's seas and their inhabitants have not experienced in millions of years. By the year 2100 the pH value of the oceans is predicted to fall by a further 0.3 to 0.4 units, and seawater thus to become one hundred to 150 per cent more acidic. That does not mean that the oceans are actually acidic, as even with values around 7.7 they are still alkaline from a chemical point of view, but they are – in relative terms – more acidic than before.

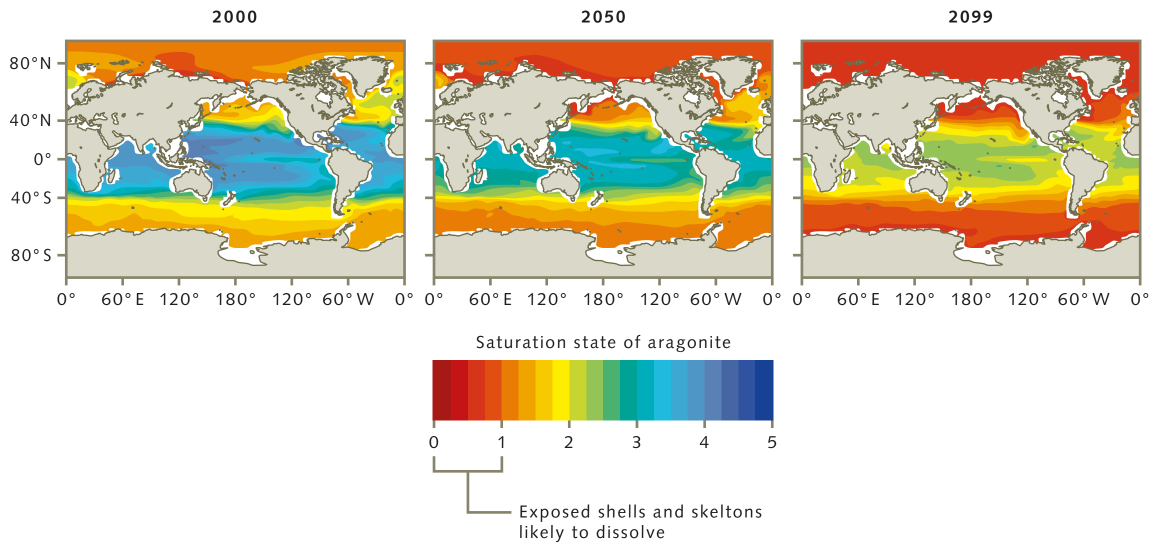
All marine creatures that breathe in water, such as fish, bivalve molluscs and starfish, have five to 20 times less carbon dioxide in their blood than land-dwellers. That is why scientists assume that water containing more carbon dioxide will affect sea creatures in a different, probably more dramatic way than species that breathe air. If the carbon-dioxide concentration in the bodily fluids of an animal rises, this leads to acidification there too and among other things impairs the transport of substances through cell membranes.

Especially at risk are calcifying organisms such as bivalve molluscs, corals, echinoderms and certain species of plankton, since they need calcium carbonates to form their shells and skeletons. The concentration of these minerals in seawater is falling as acidification increases, however. For the organisms, this means that the more acidic the water becomes, the more effort they have to expend to construct their shells and skeletons. However, the more energy the creatures invest in calcification, the less they have left for other processes essential for survival, such as growth and reproduction. Therefore, in the long term, the size, weight and overall fitness of the organisms decline. Moreover, as acidity levels rise, so too does the danger that the more acidic water will attack existing mollusc and snail shells, and coral reefs, and will damage or even totally destroy them.

Ocean acidification thus affects organisms quite directly – especially in the polar regions, where most organisms already only survive because they have reduced their energy consumption to the absolute minimum. This means that many marine dwellers have almost no energy reserves to cope with the extra pressure of acidification. What makes matters worse is that acidification and warming of the seas go hand in hand. The interaction of the two processes can either increase or decrease the impact of acidification in the ocean, depending on the species. Be that as it may, the effects on individual members of the food web indirectly influence the entire marine community.

Ocean acidification hotspots

The ice-free areas of the Arctic and Antarctic Oceans absorb more carbon dioxide from the atmosphere than the global ocean overall and acidify more quickly than warmer ocean regions. This is primarily due to the still comparatively low water temperatures of the polar seas. Gases such as oxygen and carbon dioxide dissolve more readily in cold water. In addition, the major rivers of the Arctic



4.43 > Because gases such as oxygen and carbon dioxide dissolve more readily in cold water, the polar seas are acidifying significantly more rapidly than water bodies in the mid- and tropical latitudes. As acidity levels in the polar seas rise, the concentration of vital calcium carbonates in the water falls.

carry large quantities of organic material into the marginal seas. If this is broken down by microorganisms, more carbon dioxide is produced, which accelerates the acidification of the Arctic Ocean. This is particularly true for the Laptev, East Siberian and Chukchi Seas. The melting of the great ice sheets also exacerbates the trend, since if meltwater flows into the sea, it dilutes the water masses. That means that the concentration of calcium carbonate ions falls as well. However, when algae blooms occur, carbon dioxide is removed from the sea and the pH value of the water rises again. Because of this, the pH of seawater is subject to natural fluctuations, especially in the polar seas.

Scientists can already see clear indications that the polar seas are becoming more acidic, but the response of the marine creatures there to the falling pH of the water varies considerably. For example, researchers conducting laboratory and field trials were surprised by the remarkable level of resistance shown by viral and bacterial communities. Some of the bacteria species even grew better in more acidic water than in water with a normal pH value. The phytoplankton proved similarly robust. However, the scientists do not see this as a reason for optimism because once the algae in the experiment reacted to the rising acidity levels, shifts in species assemblages fundamental to the entire food web generally followed.

Organisms benefiting from acidification include large algae such as the Arctic kelp *Saccharina latissima*, also known as sugar kelp. The increasing carbon-dioxide content of the water facilitates photosynthesis to a certain degree, so that the algae grow better. Moreover, experiments show that Arctic cold-water corals can also construct their calcareous skeleton in a more acidic environment – provided that they find enough food to meet the greater energy demand. However, scientists fear that in the long term the acidification of the water could lead to signs of decay at the base of the reefs. These are composed of limestone formed from dead corals, which could dissolve if acidity levels rise in the Arctic Ocean.

The losers from acidification, on the other hand, include the Arctic and Antarctic sea butterflies (Pteropoda). These animals secrete a calcium carbonate shell. In experiments, researchers observed that the shells were generally smaller and less stable in more acidic conditions, and exhibited greater damage than in water with a normal pH value. The green sea urchin *Strongylocentrotus droebachiensis* produces fewer young in more acidic water, because the eggs are less well fertilized. Furthermore, the number of deformities among the embryos increases. There is also a gloomy outlook for the echinoderms of the Antarctic shelf seas. These regions of the ocean are predicted to acidify so rapidly that echinoderms such as sea urchins and starfish will have to migrate into deeper waters to avoid being harmed by the higher acidity.

Second to marine mammals, fish are among the most highly developed creatures in the oceans. They have complex regulation mechanisms that enable them to adapt to changing temperatures and carbon-dioxide concentrations in the water. Fish neutralize the surplus carbon dioxide in their bodies using acidity-regulating processes in their gills, intestinal tract and liver. Biologists have studied this effect extensively and established that fish can compensate for a lower pH value within a few hours.

However, the scientists also discovered that these mechanisms only function fully in adult fish. Juvenile fish, on the other hand, are not yet able to protect themselves adequately, and react significantly to acidification of the sea; this is the case with juvenile cod, for example. In acidification experiments, smaller numbers of fish larvae were released from the egg; they were noticeably smaller at this stage than in normal environmental conditions and needed more oxygen. At the same time, twice as many juvenile fish died in the first 25 days of life at the pH values forecast for the end of the 21st century than under today's conditions. Studies using young Atlantic herring *(Clupea harengus)* showed that the juvenile fish exhibited organ damage and deformities more often in acidified water. These became more severe as the acidity of the water in the test basins increased.

Such species-specific consequences of ocean acidification indirectly alter the entire species structure of the polar seas, for example, when one species experiences a clear competitive disadvantage as a result of acidification, while its rivals remain unaffected. Biologists believe, for instance, that in the future non-calcifying algae will have considerably better conditions for growth than calcifying algae. In the long term, a development of this kind could mean that in places where large kelp forests exist today, dense carpets of a more mat-like algae will flourish in the future. Another consequence of acidification could be, however, that important limestone structures in the sea disappear – and with them the species that live on or in these structures. Especially at risk are cold-water coral reefs and mussel and maerl beds. The latter are coastal sand or shingle banks made up of more than 50 per cent ramified living and dead red algae. Mussel beds provide a source of food for many seabirds, and for marine mammals such as the walrus. Should they die as a result of acidification, a vital livelihood base will be lost, not only for the more highly evolved animals, but for humans as well.

The situation is exacerbated by the interaction of ocean acidification and rising sea temperatures. A major meta-analysis has shown that Arctic marine dwellers react more sensitively to more acidic water if their environment becomes warmer at the same time. This is the case with sea butterflies and fish. For example, if the acidification and warming of the Barents Sea continues as it has to date, the cod population there, which is of enormous importance for the fishing industry, will probably collapse by the end of this century. On the other hand, studies on Antarctic fish and sea urchins showed clearly that temperature changes put the animals under considerably more stress than the increasing acidity of the water, to which many creatures in the trials were able to adapt. Nevertheless, to do this they required a great deal of time, which they are unlikely to have in their natural environment.

The wide variations in the responses of individual species to the ongoing acidification and warming of the polar seas make it difficult for scientists to draw general conclusions. Moreover, there are no conclusive long-term studies, especially for the Antarctic, that consider multiple environmental factors. However, all findings and prognoses so far indicate that the falling pH of the water will be accompanied by fundamental changes to the biotic community, which, in the Arctic at least, will also have a direct effect on human societies.

Changes for animals on the land

Climate change is also altering the land areas in the polar regions, and therefore the habitats of their occupants, especially in the Arctic. In many regions today, the snow cover is melting much earlier in the year, the sea ice is retreating earlier and for longer durations, and the vegetation is beginning to sprout earlier in the year

4.44 > Reindeer in the Svalbard Archipelago have developed the habit of eating seaweed washed up by the sea in winters with frequent rain and frozen snow or ice covers.

because of the warmer temperatures. These changes have consequences. Researchers note that the distributional ranges of polar species are shifting northward as subarctic species advance into the southern reaches. The entire tundra is in motion; even the elk are on the move, as a Siberian reindeer herder observed more than five years ago.

In the future, the changes will probably be even more dramatic because, even if humankind is able to limit average global warming to two degrees Celsius, the air temperatures in the Arctic region will rise by 2.8 to 7.8 degrees Celsius and pave the way for species from more southern realms. The unique biological communities of the high Arctic lands are threatened with extinction in the long run because their northward retreat is limited by the Arctic Ocean. Only those polar species that are able to migrate to higher elevations or to remote islands will have a prospect of survival.

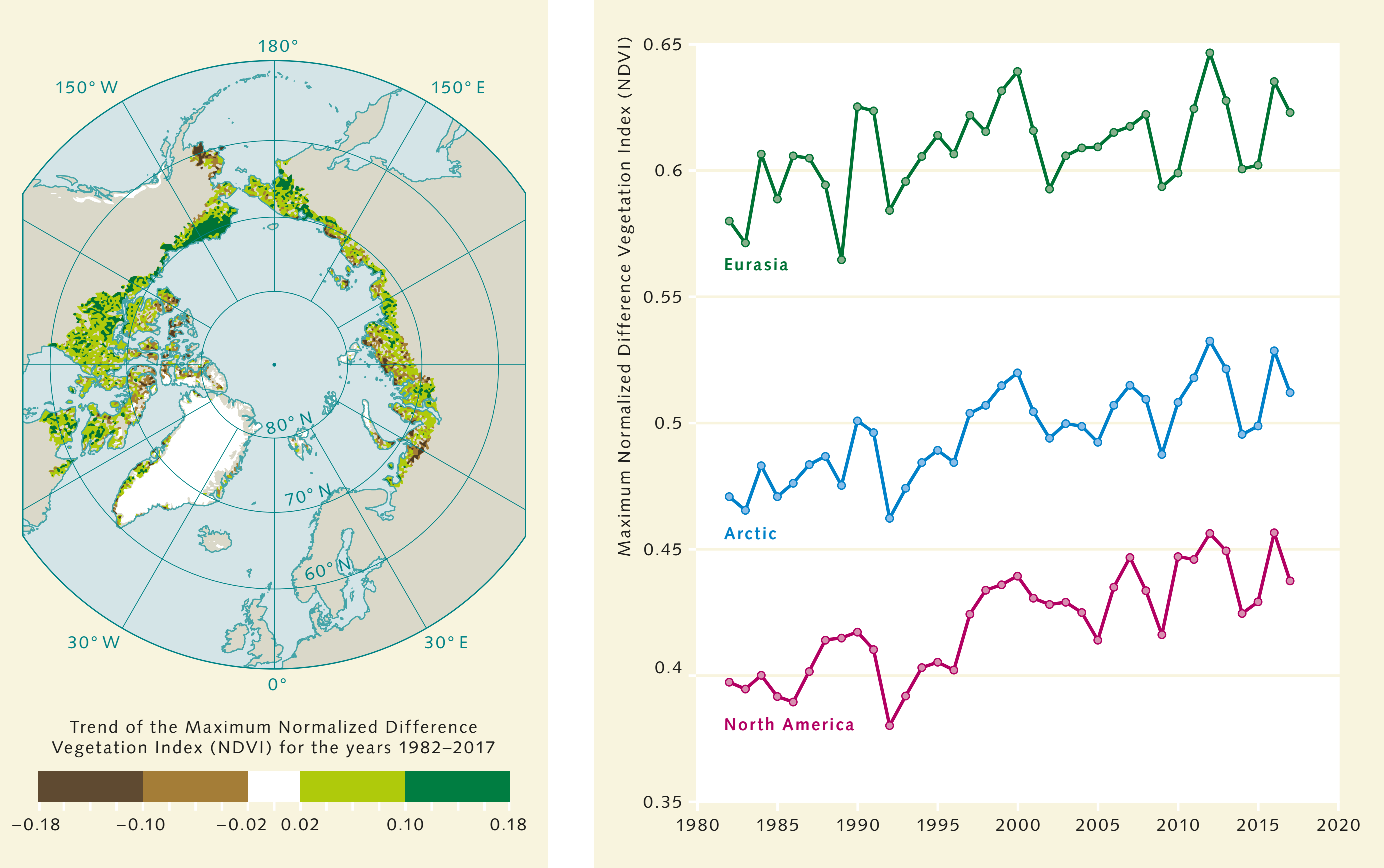
Which species survive in the Arctic in the future will primarily be determined by the winter conditions. Temperature stress and flooding due to strong rains or sudden snow melt, for example, threaten small rodents like lemmings, which in the past have been able to find protection from cold and predators beneath the snow. Ice-rain or freezing of the snow cover also hinders caribou, reindeer and musk oxen in their search for food. In this situation, the lichens, which are essential for their subsistence, are so firmly embedded in the ice that the animals cannot scratch them free with their hooves. The animals are threatened with starvation, especially the herds living on Arctic islands or in very isolated areas where there is little chance of migrating to other regions. The reindeer in western Svalbard have begun to look for food on the beaches in winters when the ground is heavily iced over. The animals wander along the coast and eat washed up kelp and other seaweed. The salty algae, however, appear to be just a stopgap solution, because in winters with normal polar weather conditions the animals again take up the search for lichens.

Increased warming in the Arctic is also disrupting nature's basic calendar. The sequence of important biological processes is undergoing a shift in time. The vegetation in some regions of Greenland is now beginning to grow 30 days earlier in the year. But the reindeer calves are still being born at the usual time because the reproductive cycle of the animals is determined by the length of the days and not by temperature. So, while the reindeer cows and their offspring were previously finding the qualitatively best food at exactly the right time, they are now showing up too late, and this has resulted in higher mortality rates for the calves.

Changes in polar vegetation

With regard to vegetation, researchers have been considering for several decades the question of whether the combination of warming and higher atmospheric carbon dioxide levels will boost plant growth in the northern polar region, or whether the increasing heat will be harmful to cold-adapted plants and rather lead to a long-term decrease in species diversity.

The answer so far has been: both, because developments are not homogeneous. In some regions of the Arctic tundra researchers have observed an increase in plant biomass (Arctic greening). This means that the plants are experiencing a boost in their metabolism, especially in response to the higher summer temperatures. They are emerging earlier and growing stronger, and they are expanding northward. This pattern is especially prevalent on the North Slope of Alaska and in the southern tundra regions of Canada and East Siberia. In these areas, bushy willows and alders grow much higher today than they did in the past. The shoots of the shrubs are thicker and the plants develop more branches and twigs. Plants like the mountain sorrel *(Oxyria digyna)* appear earlier in the year and bear larger and greener leaves, and grasses are now sprouting in many exposed sites where previously only gravel was found.



4.45 > Researchers have been using satellite data since the 1970s to observe the development of vegetation patterns in the Arctic region. With the help of this data from space they have created the Normalized Difference Vegetation Index (NDVI). The more vascular plants grow in a region, the higher this value is (Arctic greening). But when the vegetation dies, the index falls (Arctic browning).

However, there are also areas where the opposite trend is prevalent, where vegetation density and biomass are declining despite the rising summer temperatures (Arctic browning). These regions include, for example, the Yukon-Kuskokwim Delta in western Alaska, the High Arctic in the Canadian Arctic Archipelago, and the northwestern Siberian tundra. Various extreme events here, such as episodes of winter heat with sudden snow melt, icing over due to unusual winter rains, tundra fires, persistent drought or plagues by various pests in the neighbouring forests have created adverse conditions for the plants. Furthermore, with the thawing of permafrost the dangers of flooding, standing water in depressions, and erosion have increased.

Because of these varied developments, scientists are certain that climate change will generate complex interplay among the vegetation, the atmosphere, the permafrost soils, and plant-eating animals. The amount of warming alone does not determine whether the vegetation cover becomes denser and greener in a certain region. What increased plant growth does indicate is that an area is responding in its entirety to warming.

Looking to the future, it is still uncertain whether plant growth in the Arctic region will generally increase if climate change progresses to a degree such that the temperature is no longer a limiting factor for the vegetation. Computer simulations predict that the vegetation will continue to advance northward. If humankind does not drastically reduce its carbon dioxide emissions, there will only be a few areas in the Arctic by the end of the 21st century where it will still be cold enough to prevent the growth of plants. But even then, the Arctic region will probably not be a favourable environment for an abundance of plants. As long as the Earth's axis maintains its tilt, the winters in the polar regions will continue to be long and dark, and the summer growing season will be so short that it will present a huge challenge to plant growth.

Risk escalates with rapid change

It has taken millions of years for the Arctic and Antarctic animal and plant worlds to adapt to the extreme living conditions in the polar regions. By comparison, the present climatic changes driven by global warming are happening so fast that the polar ecosystems and their highly specialized organisms are in danger of not being able to adapt quickly enough. Human-induced climate change therefore poses a massive threat to the diversity of polar biological communities and to their functionality.

Today, we know that the feeding interrelationships in the polar ecosystems are much more complex and diverse than was previously understood. Similarly, we still know relatively little about the biodiversity of many groups of polar organisms. In 2014, for example, scientists had sufficient information on less than two per cent of the Arctic organisms to be able to recognize climate-induced changes in their behaviours. The researchers are therefore still unable to say much about the possible reactions of the affected biological communities. In the areas that have been well researched, however, one thing is very clear: Where climate change is already having an impact, the natural polar biological communities look different today than they did prior to industrialization.

4.46 > On Herschel Island in far northern Canada, plant growth has increased in the wake of climate change, as these two photographs illustrate. The image on the left was taken in 1987 and the one on the right two decades later.

CONCLUSION

Highly specialized and greatly threatened

Cold, light and ice determine the course of life in the Arctic and Antarctic. On land, these parameters are the reason that the growth or reproduction cycles for most organisms are very short, and that many animals leave the polar regions at the end of the summer. In the sea, the cold makes energy-efficient slowness essential, which in turn can make many organisms quite long-lived. The amount of sea ice, the food supply, and access to open water change in rhythm with the polar day and night.

Under the pressure of extreme environmental conditions, highly adapted biological communities with amazingly high biodiversities have developed in both polar regions, although the number of species does not begin to approach the dimensions of the tropical regions. In the Arctic, the greatest biological diversity is found on the land because of the relative distribution of the ocean and continents. In the Antarctic, on the other hand, almost all life is dependent on the sea. The degree of adaptation here and the number of endemic marine species are both significantly higher than in the Arctic. This is due to the geographic isolation of Antarctica and to its longer and more diverse glacial history.

The recurrent growth of Antarctic glaciers and ice shelves out to the continental margin has often brought the dwellers of the shelf seas to their physiological limits. Over time, this has resulted in the development of many new and highly specialized species, a process that scientists refer to as a species diversity pump. The inhabitants of the Arctic Ocean, on the other hand, were able to migrate to the North Pacific and North Atlantic in times of extensive icing. Today researchers can distinguish the Atlantic and Pacific sectors with regard to the marine ecosystems of the Arctic Ocean.

Plants overcome the cold and the shortage of light in various ways. These include cellular frost-protection mechanisms, a compact size, slow growth, heat-optimizing characteristics such as hairs or flower shapes, accumulation of large reserves, improved photosynthetic performance, largely asexual reproduction and multiple utilization of nutrients.

In endothermic animals, an insulating winter coat or plumage prevents the loss of valuable heat. They build large reserves of fat, warm each other when necessary, and survive extreme weather conditions in sheltered locations. Many ectothermic marine organisms utilize anti-frost proteins, move in energy-saving mode, grow slowly and produce comparatively few offspring, which they provide with the best possible conditions in early life.

But due to climate change, the physical foundations of life in the Arctic and Antarctic are shifting. Their polar ecosystems and highly specialized organisms face the imminent risk that they will not be able to adapt rapidly enough to survive. With the disappearance of sea ice, a habitat is vanishing that serves many species as a sanctuary, food source and hunting ground. These organisms are now threatened with extinction. Rising water temperatures are increasing the energy requirements for ectothermic organisms, while also paving the way for immigrant species. Food webs are becoming destabilized, and competition for food is intensifying. Acidification of the polar seas also makes survival more difficult for organisms that build calcareous shells or skeletons. Climate change thus poses a massive threat to the biodiversity and functionality of polar ecosystems.