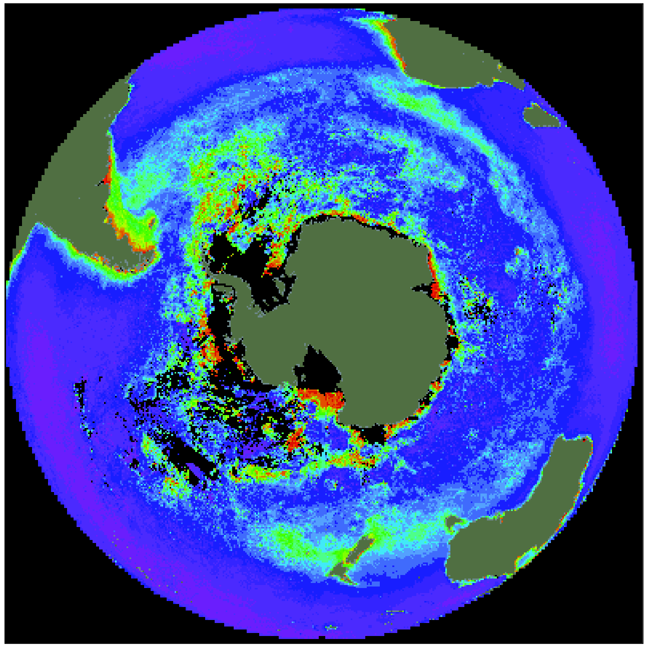
Southern Ocean productivity – control and feedback

Resource M1



Source: NASA/GFSC

Composite satellite image of phytoplankton abundance between 1978 and 1986. 'False' colours code for low (blues and purples) and high (yellow and orange) densities.

Phytoplankton growth in the Southern Ocean

Minute floating plants – the phytoplankton – provide the energy supply for the Southern Ocean ecosystem. Because they remove carbon dioxide (CO_2) dissolved in the water, phytoplankton may ultimately control the composition of the atmosphere and hence affect climate. Primary production varies over the Southern Ocean, and is controlled by environmental and other factors. Satellite observations allow us to map the large-scale distribution of phytoplankton.

This resource examines the control of phytoplankton production in detail, in relation to ecosystem function and how phytoplankton carbon uptake interacts with climate. Controlling factors can be grouped under three headings – the energy supply for growth; nutrients which supply such elements as nitrogen, phosphorus and silicon, and removal of phytoplankton biomass. Several of these factors interact: a simple example of this is provided later.

Light and phytoplankton growth

Phytoplankton grow by photosynthesis like other plants. Light energy is used to build complex organic compounds from simple materials. Phytoplankton absorbs light as it passes down the ocean, using the green pigment chlorophyll. Water with few phytoplankton or other particles is clear, but only about 1% of surface light reaches 100 m depth. Light penetration is much less in turbid water.

So phytoplankton growth is restricted to the top few tens of metres in the ocean: about 2% of the average depth of the Southern Ocean. Phytoplankton which sink deeper get too little light and stop growing. If the wind-mixed upper layer is deepened by a storm, phytoplankton growth is reduced. Shallow mixed layers typical of sheltered coastal areas allow better phytoplankton growth.

Ice cover cuts down the light entering the water. Sea ice and the snow on top can filter out 99% of the light. Few phytoplankton are found beneath the ice, although algae trapped within the ice can be abundant. When ice melts in spring, the fresh-water produced may form a shallow, stable layer where dense phytoplankton blooms develop.

Large-scale patterns

The amount of light available not only varies with local conditions but is also determined by the time of year and where you are. At the Equator, the amount of sunshine received during a day is similar throughout the year. As you travel towards the South Pole, the seasons become very different. At the Antarctic Circle (66°S), there is total darkness at mid-winter (21 June) and 24 hours daylight at midsummer (22 December). Differences between seasons is increased further in the Southern Ocean by the development of sea ice.

Temperature is another obvious controlling factor: it is well-known that the growth rate of phytoplankton decreases at lower temperatures. However, phytoplankton can reach high densities in polar waters, so that temperature as a direct limiting factor for growth has generally been discounted. It may have more subtle effects, which will be referred to later.

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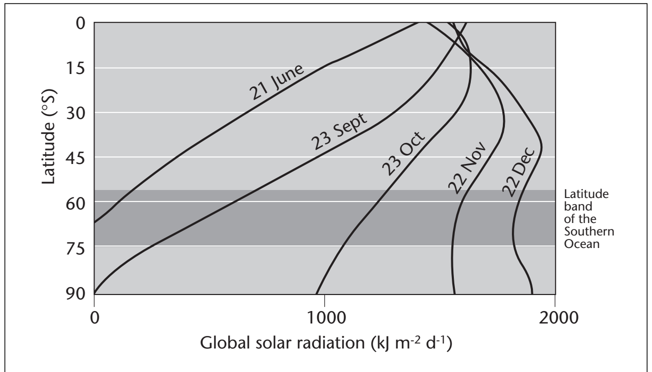
Two contrasting light environments for phytoplankton: melting ice produces a stable layer where light is high (upper picture), strong winds cause deep mixing and low light (lower picture)



The amount of daily sunlight received varies with latitude and time of year

Phytoplankton growth and other elements – the Antarctic Paradox

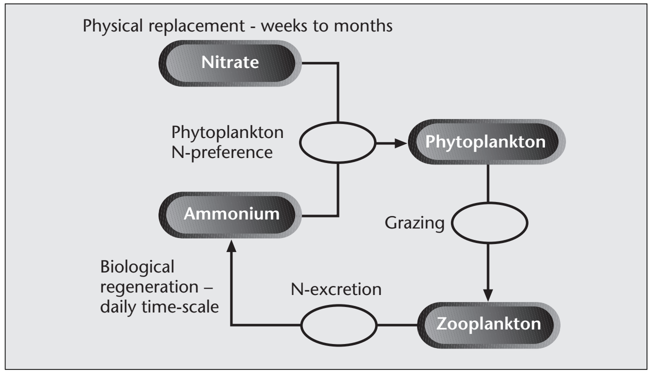
Over much of the world's oceans availability of elements other than carbon ultimately limits primary production. These elements – nitrogen, phosphorus, silicon – are also used for phytoplankton growth. They are used completely during spring and summer, and replaced during the following winter. However in a few ocean regions phytoplankton growth is low but these nutrients remain abundant. These are High Nutrient – Low Chlorophyll (HNLC) environments. The Southern Ocean is the largest HNLC region.

We have seen that energy supply might reduce phytoplankton growth rate, and thus make them unable to use the nutrients. A new factor is now being studied. While the nutrients such as nitrogen may be readily available, it is now suspected that a shortage of trace elements may limit growth. Trace elements carry out essential functions but are needed only in tiny amounts. Some metals form parts of enzymes – biological catalysts. Experiments in the Southern Ocean have shown that addition of dissolved iron stimulates phytoplankton growth. Macronutrients are rapidly removed, and the local uptake of CO_2 from the air also increases.

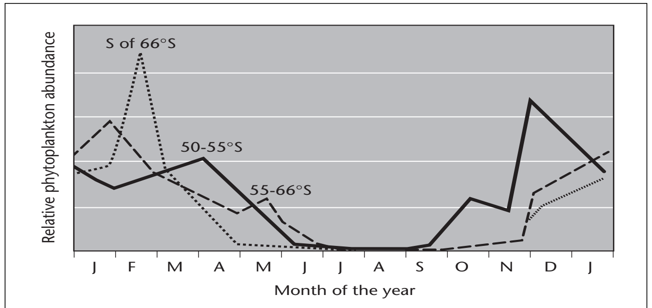
Interactions between controlling factors

It is always assumed that the high concentrations of nutrients in the Southern Ocean can never limit growth. We have noted that these nutrients typically remain at high concentrations during summer. However, this is based on the view that these nutrients are fully available to the phytoplankton.

Here we examine part of the nitrogen cycle. Nitrogen is biologically important: about 15 nitrogen atoms are taken up for every 100 atoms of carbon. Uptake of nitrogen may be a significant control of phytoplankton growth. The dominant form in seawater is nitrate (typically 80–95% of total dissolved nitrogen), which comes from deeper water (Resource M2). Temperature may affect the way in which nitrogen nutrients get into phytoplankton cells. Nitrate is taken up through processes which require energy. In the cell, nitrate has to be converted into ammonium before it can be used. This conversion, which also requires energy, uses iron in an enzyme. This is one reason why phytoplankton in the iron-poor Southern Ocean cannot use all of the available nitrate.



A simple nitrogen cycle – nitrogen is taken up by phytoplankton both as nitrate and ammonium. Zooplankton excretes ammonium, providing recycling and feedback control



Seasonal change in phytoplankton abundance in three zones of the Southern Ocean

Ammonium, the cell's natural nitrogen supply, is also present. Using ammonium costs less in energetic terms, but ammonium is comparatively scarce, there is only a few days' supply in surface water. Some of this is nitrogen removed from dead phytoplankton by microbial activity. Microbes can recycle nitrogen very rapidly. The grazing animal plankton also play an important role in recycling nitrogen, because they excrete ammonium. The high ammonium concentrations produced by microbial and zooplankton activity may suppress nitrate uptake.

Thus the type and amount of nitrogen used by phytoplankton responds to several factors – temperature affects nitrate uptake, ammonium also inhibits nitrate use, and ammonium increases phytoplankton growth. The importance of these processes can be seen in areas where the abundance of one key zooplankton species – krill – varies. In most years, ammonium production is high. Nitrate concentrations remain high because phytoplankton grow rapidly using ammonium. In a few years, krill abundance is about 15% of normal. Then ammonium concentrations are lower, and nitrate is removed more effectively by slow-growing phytoplankton.

Food web

A Energy from sunlight fuels phytoplankton **1** growth

B **Carbon dioxide** enters surface ocean from atmosphere

C **Organic material** produced by photosynthesis, some recycled by other microbes **2** **3**

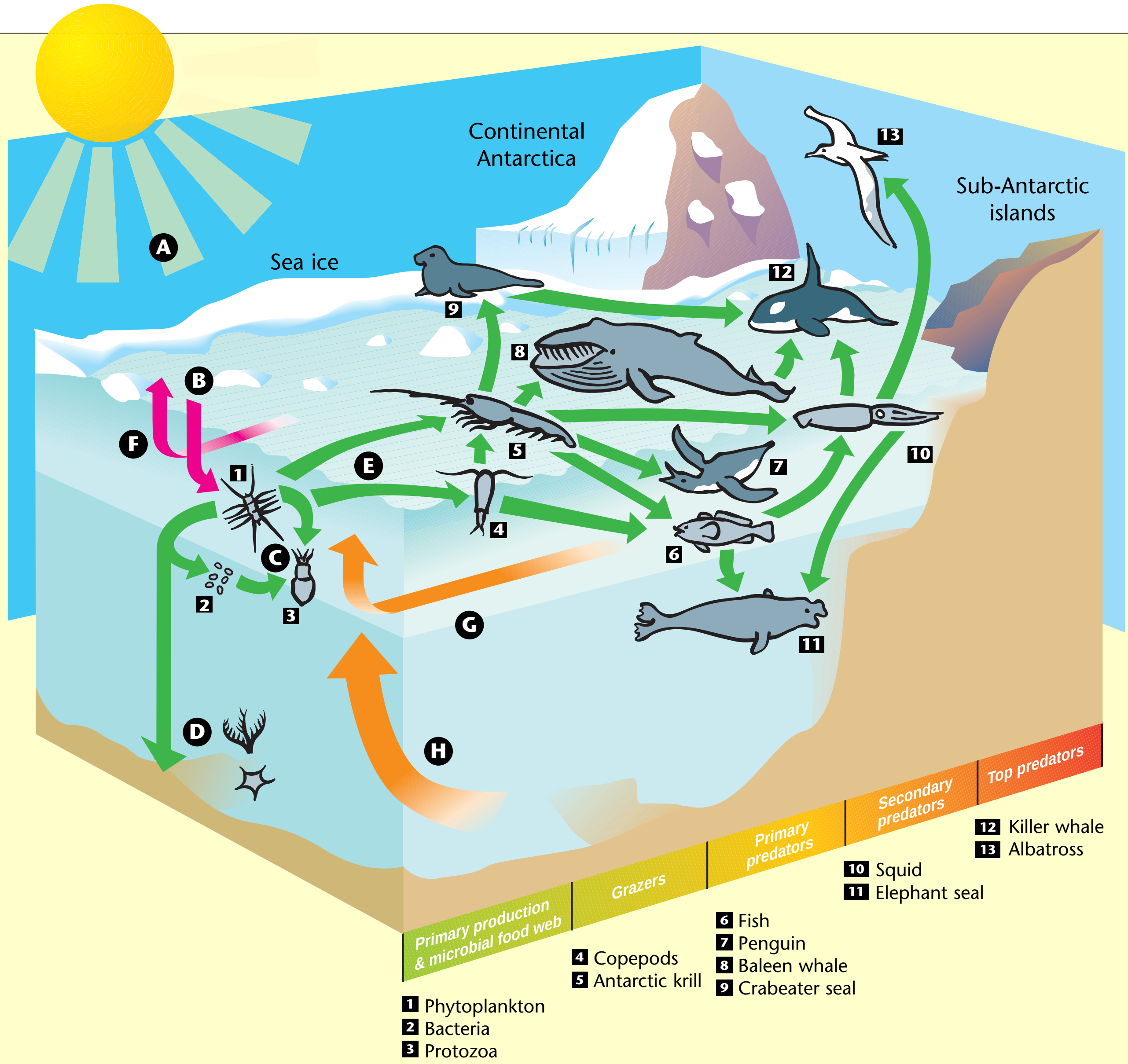
D Up to 10% of **organic material** sinks to deep water to feed bottom – dwelling animals

E Most **organic material** passes through the food web **4**–**13**

F Respiration releases **carbon dioxide** which can return to the atmosphere

G Other elements, such as **nitrogen** and **phosphorus** are also recycled

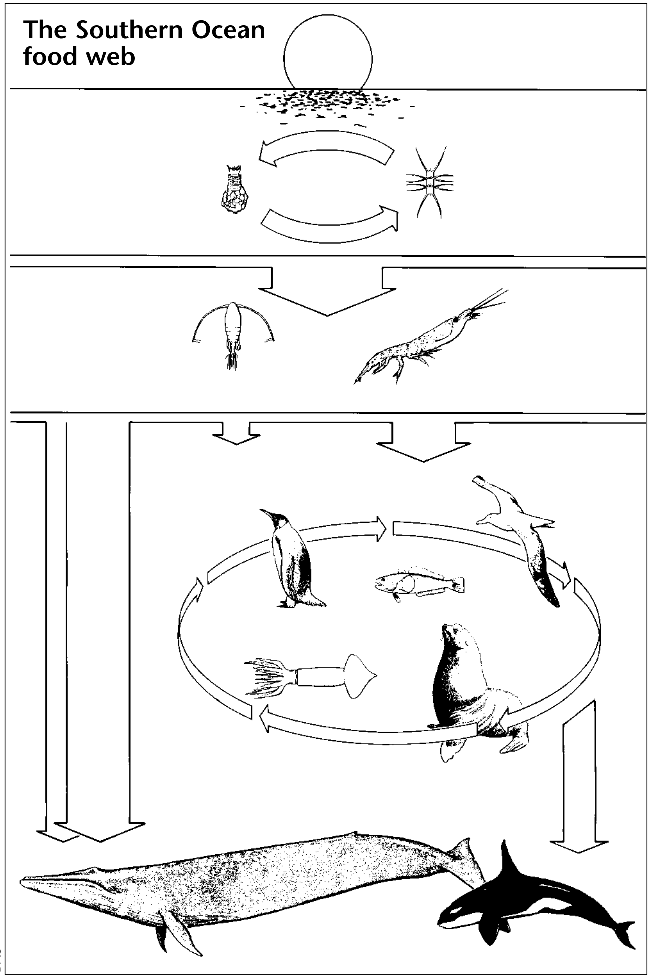
H There is major input of **nitrogen** and **phosphorus** by upwelling of more northerly deep water



Plants and animals in the Southern Ocean

Some key species and groups

Phytoplankton are single-celled or colonial plants, 1 µm to 1 mm in size. 'Primary production' is used by other members of the food web for growth and energy. Various consumers feed on the phytoplankton. Some of these are other microscopic organisms such as protozoa. These feed and grow rapidly, and may remove much or all of the primary production.



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Larger animal grazers are often dominated by crustaceans. The most important groups are copepods and krill. Krill are shrimp-like animals which may live for 6–7 years and grow to 6 cm long. They form dense 'swarms' which may be hundreds of metres across and contain millions of krill. Krill dominates the diet of several predator groups in the Southern Ocean.

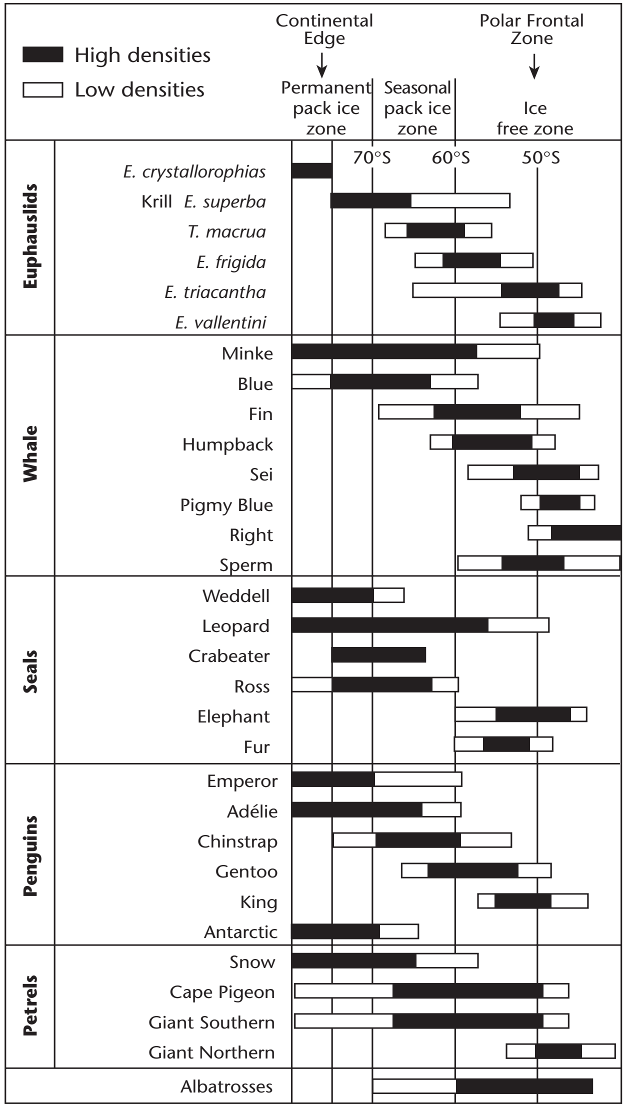
Some predators are fully aquatic, such as fish and squid. Fish in the Southern Ocean belong to a specialised group which has evolved in the region. Their growth tends to be slow and they take a long time to mature and breed. By contrast, squid are very active animals which complete their life-cycle in one or two years. They are molluscs, but have evolved to be effective predators. They have excellent eyesight, and swim fast to catch their prey.

Warm-blooded animals – birds and mammals – are a very conspicuous part of the fauna of the Southern Ocean. These have very high metabolic rates to maintain their body temperature, so must eat a large amount of food to support themselves and their offspring. Some species are only summer visitors to the Southern Ocean.

Bird groups include penguins, albatrosses and petrels. Penguins are primitive birds which have become flightless. They swim fast and can dive to depths of 100 m. Many are krill feeders although the larger species, feed on fish and squid. All birds have to breed on land.

There are six seal species in the Southern Ocean, including the krill-eating crabeater seal which is the world's most abundant species, with an estimated 12 million animals. Some seal species, including the crabeater, live and breed in the pack ice zone.

The largest mammals are the whales. The toothed whales feed mainly on fish and squid, and include the sperm whale and the killer whale. The baleen whales are filter feeders and feed on the huge numbers of krill.



The geographical zonation of selected species from the Antarctic continent northwards

Source: Laws, R. redrawn in Hansom, J.D. and Gordon, J. E. (1998) Antarctic Environments and Resources. Longman, Harlow.

Adaptations to life in the Southern Ocean

The Southern Ocean seems to be an inhospitable environment, but contains a rich community of animals and plants. In many cases, survival is achieved through conserving energy by slowing down body processes. However, Antarctic marine animals can be just as active as their relatives in warmer waters.

Two principal and interrelated features of the Southern Ocean environment are biologically important. The uniformly low temperatures can have a direct effect on the rates of biological processes. Food supply is markedly seasonal, because the sunlight needed to fuel the plants on which the food web is based is only sufficient for growth in summer. The effects of these factors are highly complex and vary depending upon the species studied and its place in the food chain.

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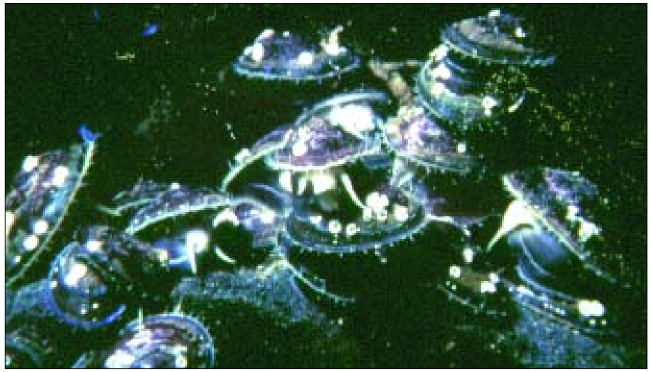
Icefish contain no haemoglobin (oxygen carrying pigment)

The growth rate of Antarctic marine invertebrates is regulated more by food availability than by low seawater temperature.

The short-lived abundance of food in the spring and early summer triggers a surge in activity in marine animals. Usually, reproduction is the first priority, and eggs and sperm stored and matured over the winter are released. This is followed by a period of intense growth, repairing damage and preparing for the six to eight months of winter ahead. As skeletal structures, such as shells, are laid down in layers, similar to the rings in a tree, growth in a particular season or year can be measured. This reveals that the very short growth period means that most resources are channelled into reproduction and storage, and little growth occurs.



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Antarctic limpets are very slow-growing animals

Reproduction is without doubt the most energy consuming of these uses of food supply, so it is not surprising that these animals only grow slowly. The Antarctic limpet, for instance, increases in size by approximately 0.3 mm per year, whereas for a similar species from our own latitudes this amount would represent a growth period of about two weeks. Molluscs in the Antarctic are typically thin shelled and very long lived. Fish are also cold-blooded and are similarly affected by environmental conditions. One group of Antarctic fish, called icefish, is unique in that they have none of the red proteins present in the blood and muscle of other creatures. These substances, haemoglobin and myoglobin, carry oxygen. Icefish manage very successfully without them because the cold water has more oxygen dissolved in it than warmer waters. The blood of icefish is clear and their flesh is usually pale – hence their name. Another adaptation found in Antarctic fish is an antifreeze protein in the blood and body tissues. Without it the fish would freeze at the temperatures experienced in much of the Southern Ocean.

Adaptations in the warm-blooded birds, whales and seals are different from those in cold-blooded fish. These animals need to control heat loss from their bodies to the cold water or air. A layer of fat, called blubber, provides insulation beneath the skin in seals and whales. Fur seals and birds have additional insulation provided by the air layer trapped in fur and feathers. Size is also important since heat loss is related to the surface area of the animal but heat generation is related to volume. Large animals have a smaller surface area for their weight than small ones.

Young animals tend to be born large and grow very fast – seal pups are weaned after a few weeks and increase weight by as much as 10 kg per day. This means that they reach a large size, rapidly giving more efficient heat conservation. Social behaviour also counteracts the cold. Emperor penguins huddle together to conserve heat and each penguin takes a share in standing in the cold outside the group.

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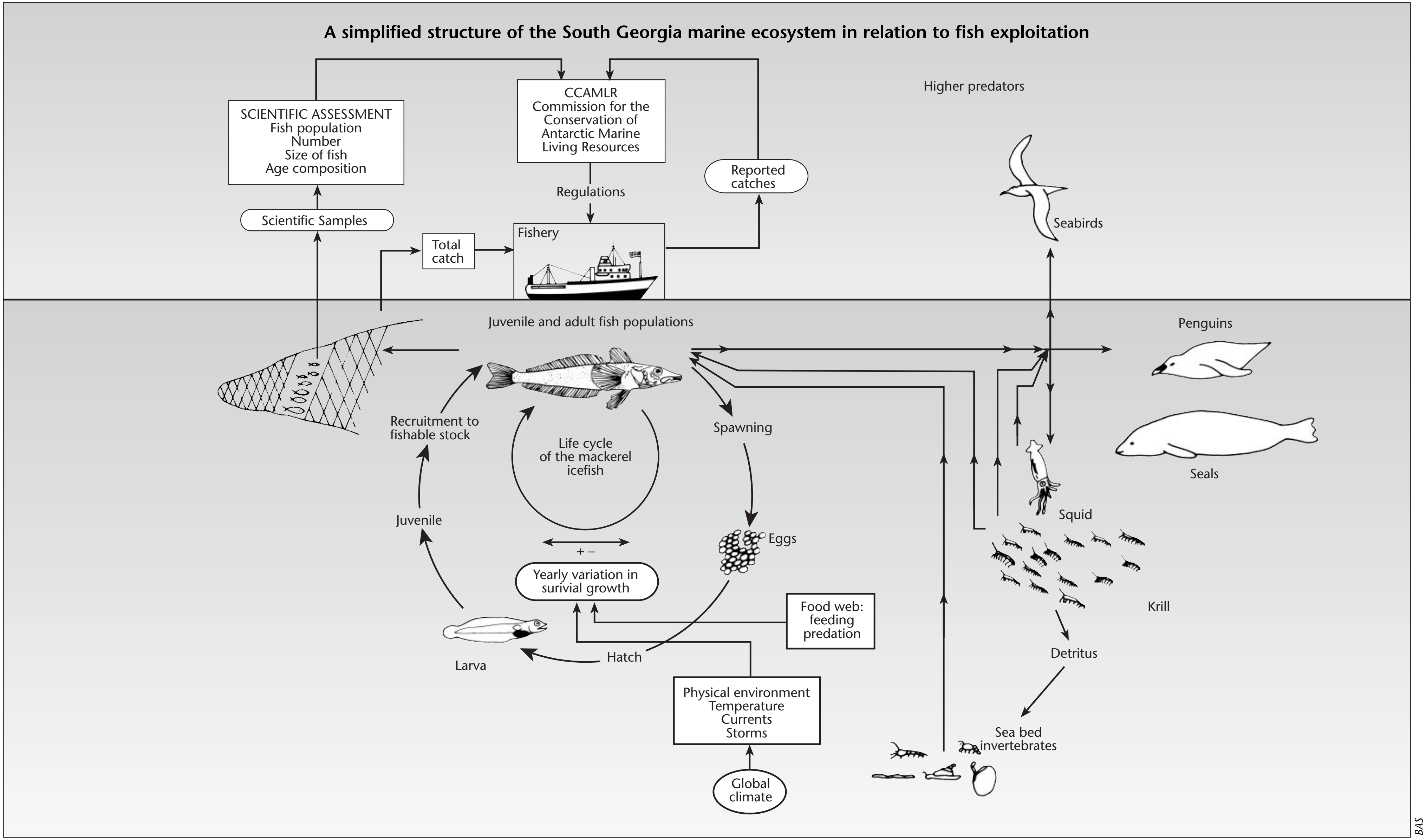
Crabeater seals are insulated by a thick layer of blubber

The South Georgia marine ecosystem



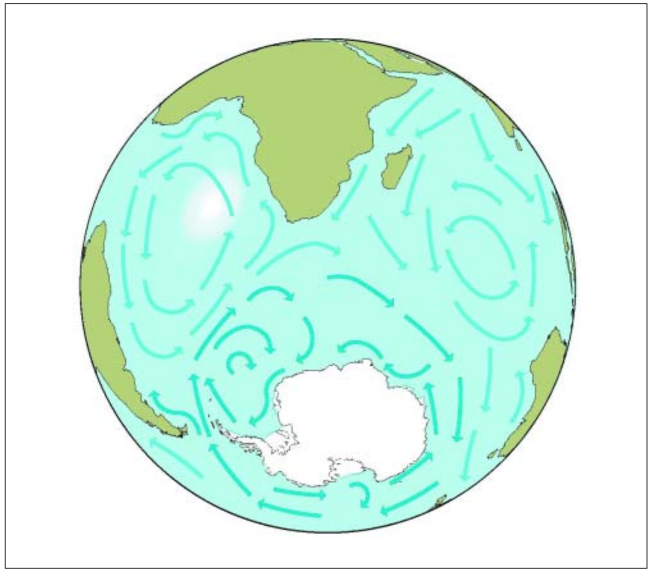
Marine ecosystems

The Southern Ocean encircles Antarctica. It forms around 10% of the world's ocean area, and extends from the continent northwards for some 2000 km to the Antarctic Polar Front. This front (called the Antarctic Convergence in earlier descriptions) forms the interface between the Southern Ocean and the South Atlantic, South Pacific and Indian Oceans. Water temperatures range from around -1.8°C in the south to 3.5°C at the Polar Front. The Antarctic Circumpolar Current is the largest ocean current in the world, carrying about 3 million cubic kilometres of water per year eastwards (clockwise) around Antarctica. Closer to the continent, flow is to the west in the Antarctic Coastal Current. However, features such as the Antarctic Peninsula and the embayments of the Weddell and Ross seas cause more complex circulation patterns. This worksheet examines physical and chemical features of the Southern Ocean environment, marine food webs, and the special adaptations which allow organisms to survive there.

Biological productivity

The success of living organisms is determined by several factors. Physical factors are important controls on determining both distribution and growth in the oceans. This is especially the case for smaller plants and animals – the plankton – which drift with the currents. Microscopic plants – phytoplankton – provide the material and energy for the rest of the ocean ecosystem.

Light availability is clearly important for phytoplankton growth, because sunlight provides the energy source which allows plants to convert carbon and other elements into living material. Resource M1 looks in more detail at how light varies in the ocean, and how this is linked to large-scale factors, such as season and position on the Earth, and to small-scale factors such as weather and sea ice cover.



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Surface circulation pattern in the Southern Ocean (dark blue arrows) and adjacent ocean basins (light blue)

Task 1 Resource M1 shows how abundance (biomass) of phytoplankton changes over the year at three bands of latitude in the Southern Ocean.

- Explain how physical factors control the amount of light available to phytoplankton, and why this causes the different seasonal patterns of abundance.

Biological processes are also important in controlling phytoplankton growth, and determining how carbon is passed through the food web. Grazing animals which feed on phytoplankton can control abundance and production. These animals may also alter the composition of the nutrient salts needed by the phytoplankton. These plants and their grazers may be a complex mix of positive and negative feedback (see Resource M1).

Task 2 The Southern Ocean has high levels of nutrient elements (such as nitrogen, phosphorus and silicon) but phytoplankton growth appears to be low.

- List some possible explanations for the High Nutrient – Low Chlorophyll (HNLC) paradox. Summarise evidence for and against the importance of each explanation.
- Construct a chart or diagram that summarises how phytoplankton growth is determined by these controls.

Food webs

The interactions between different species in an ecosystem are described by a food web which shows 'who eats whom'. A simplified food web for the Southern Ocean ecosystem is provided (Resource M2). This not only shows the diet of various species, from herbivores like copepods to the top predators like killer whales, but traces the cycles of the major elements carbon, nitrogen and phosphorus.

Task 3 Resource M3 contains a diagram of the Southern Ocean food web. Copy this diagram and label each species group. The text in this resource, and Resource M2, will help you.

- What are the different levels in this diagram? (Compare with Resource M2).
- Note which animals are linked to the land for part of their life-cycle, and explain how.
- Describe the importance of krill in the ecosystem.
- Which species would be affected by changes in krill abundance (Resources M2 and MC1 with Worksheet 13 may assist you)?

Carbon and energy flow in the ecosystem

The food web describes the flow of material (usually expressed as carbon), and thus energy, from the microbes right up to the top predators. This transfer is inefficient.

Only about 10% of food eaten goes to growth and reproduction, and the other 90% provides energy for life processes. However, this efficiency varies from group to group. Use of phytoplankton carbon by other microbes can be 40% efficient, whilst only 3 or 4% of the food eaten by seals and penguins is used in growth and reproduction.

Task 4 The food web diagram in Resource M2 has five levels – primary producers and microbes, grazers, primary predators, secondary predators and top predators. On average, the microbial community 'fixes' 50 tonnes of carbon over each 100 square kilometres of sea surface per year.

• Assume that 90% of the carbon is used for energy rather than growth when food goes from one level in the food web to the next. How much growth (in tonnes of carbon) would a top predator species like the killer whale produce in the same 100 square kilometre area over a year?

Distribution of species

For some species, especially the plankton, distribution is determined by seawater temperature and ocean currents. Antarctic krill is an example. Its natural habitat is the cold waters of the Antarctic Current. Where the current moves northwards, krill are carried into slightly warmer waters, but they are not found north of the Polar Front.

Larger animals have greater control over where they are and where they are going. Some birds and mammals migrate long distances, travelling into the Southern Ocean during the southern summer to breed, and to feed themselves and their young. In winter they migrate to warmer waters. These animals live close to their food supply, but other factors such as the availability of suitable breeding sites affect their distribution.

Task 5 Study the chart of the distribution of various animals which appears in Resource M3. The first category of animals are euphausiid crustaceans, including Antarctic krill *(Euphausia superba)*, which are eaten by many of the predators. A map of the distribution of krill is given in ➤

➤ Resource MC1 (with Worksheet 13) – you can compare this with the latitude range shown in the table.

• Blue whales, crabeater seals, fur seals and chinstrap penguins are all mainly krill predators. Compare their distributions with those of krill. Is the distribution of their food the only factor which determines where they live?

Interactions between predators and prey

When Antarctica was first explored, the wealth of animal life aroused considerable scientific and commercial interest. It seemed strange that such a hostile environment should be so productive. Later it was found that phytoplankton production over much of the Southern Ocean is low. So how could the abundant wildlife survive on low primary production? Part of the answer lay with the structure of the food web. Large grazing animals such as krill, in dense swarms of thousands of individuals, are big enough to be fed on by much larger animals, and thus form a very efficient link between plant growth and large predators.

Hunting of the great whales in the first half of the twentieth century may have halved predation pressure, perhaps making hundreds of millions of tonnes of krill available to other predators.

In some years, krill abundance in parts of its range is lower than usual. Resource M1 shows that this has an impact on primary production. It also has considerable impact on krill predators. Breeding by penguins and seals in the affected areas can be less than 10% of normal levels.

Adaptations to the Antarctic marine environment

The Antarctic marine environment presents difficult conditions for life, with limited solar radiation, low temperatures and a short summer season. Living things have acquired several special characteristics during their evolution. The range of adaptations is considerable, and varies from changes in body chemistry to modified breeding behaviour (Resource M4).

Task 6 With reference to Resource M4, make a table of adaptative mechanisms. Related mechanisms should be grouped into categories – biochemistry and physiology; body structure and feeding; and life-cycle and breeding. Each section should contain three columns – the adaptive mechanism, its function, and the species which use it. An example of a body structure mechanism would be:

Adaptive mechanism	Function	Example
Fat and blubber	*Retaining body heat*	*Seals and whales*

Human impacts on the Southern Ocean ecosystem

Human activity in Antarctica, especially fishing, can cause impacts on various marine species. Sustainable management of Southern Ocean fisheries requires extensive knowledge of the marine ecosystem.

Other human activities, some remote from Antarctica, can also bring about changes. Biological processes in the Southern Ocean, such as fixation of carbon dioxide by phytoplankton, may in turn modify the global environment.

Task 7 Resource M5 shows how a commercial fishery in the ocean ecosystem near South Georgia interacts with local predators. The mackerel icefish is the subject of a commercial fishery as well as being food for a range of predators. Icefish and other predators may compete for krill, whose population fluctuates through natural causes. Krill is also fished commercially in this region.

• Identify the ways in which human activity can affect the ecosystem, both directly and indirectly. Which of these effects appears to be closely controlled, and which only poorly or not at all?

• Consider both local and global impacts, including such factors as global pollution, climate change and ozone destruction.

Fishing in the Southern Ocean is discussed in detail in Worksheet 13 on Management and Conservation of Marine Species.