other than autocatalysts. Temporal trends in the data show that although the concentrations of Ag and Pb in Boston Harbor sediments are decreasing, likely due to the cessation of sewage release, concentrations of Pt and Pd are either stable or increasing with time. This trend is consistent with a significant input of these metals from nonpoint sources such as the release of untreated road run-off. The impact of human activity on levels of dissolved Pt and Pd in coastal waters is not well documented. Similarly, in the marine environment, the chemical form of anthropogenic PGEs, and the extent to which these metals are subject to biological uptake are also poorly known. These gaps in our knowledge of the marine chemistry of the PGEs will likely influence the future direction of marine PGE research.

Summary

The PGEs are among the least abundant elements in sea water. The low concentrations of these metals in sea water reflect their generally low concentration in earth surface material rather than uniformly low solubility. Although there is a general consensus regarding the approximate concentrations of these metals in sea water, their vertical distribution in the water column remains controversial and poorly documented. Improving our understanding of the marine chemistry of the PGEs both in the water column and in marine sediments is important to interpreting the marine Os isotope record, exploiting PGEs as tracers of extraterrestrial material in marine sediments, and understanding the consequences of anthropogenic release of PGEs to the marine environment.

See also

Glacial Crustal Rebound, Sea levels and Shorelines. Satellite Altimetry. Sea Level Variations Over Geologic Time.

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POLAR BEARS

See **MARINE MAMMAL OVERVIEW**

POLAR ECOSYSTEMS

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Introduction

The Arctic Ocean and the Southern Ocean together comprise a little under one-fifth of the world's oceans (the precise fraction depending on how these oceans are defined). The two polar oceans are similar in being cold, seasonal, productive, and heavily influenced by ice, and both have long been fished by man. They differ markedly, however, in geography, age, and many aspects of their biology.

In both polar oceans sea water temperatures are typically low, and in many areas are close to freezing ($-1.86°C$) for long periods. In areas of seasonal ice cover the surface waters undergo a summer warming, but even at the lowest latitudes this rarely amounts to more than a few degrees. Typically summer sea water temperatures in the seasonal sea ice zone of Antarctica are between $+0.5$ and $+1.5°C$.

The inclination of the earth's rotational axis means that the seasonality of received radiation increases towards the poles. This seasonality, exacerbated throughout much of the polar oceans by the accompanying seasonal ice cover, means that primary production (the conversion of inorganic carbon and other essential nutrients into organic matter by plants) is also intensely seasonal.

The combination of a low and fairly seasonal temperature with a highly seasonal primary production (**Figure 1**) distinguishes polar marine ecosystems from all others on earth. Temperate systems are typically also highly seasonal, but here both temperature and primary production tend to covary. Tropical marine ecosystems experience high temperatures that are fairly aseasonal, but there are often strong seasonal variations in other important environmental variables (for example, rainfall and fresh water run-off in monsoon areas).

These features of the polar regions set two particular challenges for organisms living there. The first is that the low temperatures will tend to slow the rates of many biological processes. This does not apply to mammals and birds, whose internal body temperatures are maintained by metabolic processes; for these endothermic ('warm-blooded') organisms the challenge is to avoid losing heat, which they do by a variety of mechanisms but principally by enhanced insulation. The subtle molecular mechanisms used by ectothermic ('cold-blooded') fish, invertebrates, plants, and bacteria are the subject of extensive physiological investigation. Despite these adaptations, however, it is a widespread observation that many important biological processes proceed slowly in polar systems. The second challenge for polar organisms is that the marked seasonality of primary production means that many of these processes are constrained to the summer months. These two features of generally slow physiological rates and intense seasonality together have a profound influence on the structure and dynamics of polar marine ecosystems.

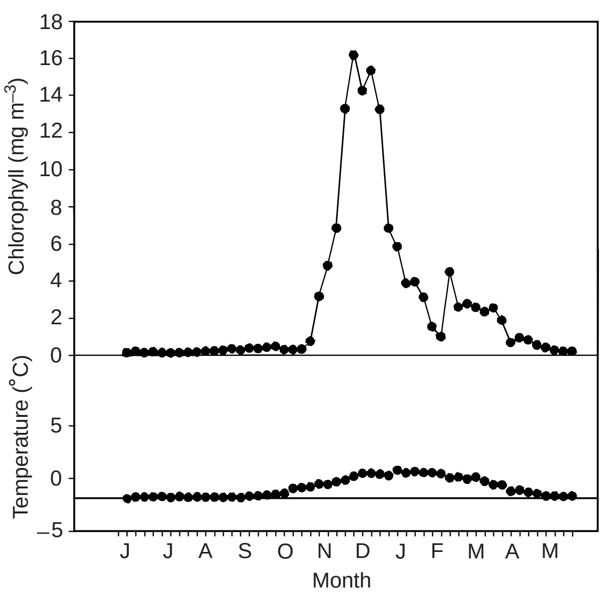

Figure 1 Seasonal variation in chlorophyll biomass ($>0.2\,\mu m$) and temperature at a typical polar locality (Signy Island, maritime Antarctic, 60°S). Both plots show weekly means over the period 1988–1994. The horizontal lines show zero chlorophyll biomass and $-1.86°C$ (the equilibrium freezing point of sea water). The marked seasonality of chlorophyll biomass coupled with the small annual variation in water temperature is typical of polar oceans.

General Features of Polar Marine Food Webs

Food webs can be constructed to emphasize different aspects of their structure or dynamics (for example, to highlight trophic interactions, energy flux, or biomass). When comprehensive, such food webs can be extremely complex. There is, however, usually a basic underlying structure, and a simplified food web for all marine systems can be produced (**Figure 2**).

The key feature of this basic structure is that it is nonlinear; energy fixed by marine plants (principally phytoplankton but also macroalgae in shallow water areas) passes in three important directions. These are (1) to planktonic herbivores and through a sequence of higher trophic levels eventually to top predators (including man); (2) to the microbial loop; and (3) through vertical flux (sedimentation) to the benthos. In deeper water the flux passes through the vast range of the midwater before reaching the abyssal plain. This basic structure applies to all marine ecosystems, but there are a number of extra features that are peculiar to polar regions. Particularly important are the influence of sea ice, the dominance at times of short linear food chains, and the importance of top predators.

Sea Ice

Sea ice has profound and pervasive effect on polar marine ecosystems. It forms a barrier to the exchange of energy, momentum, and gases, thereby acting as a major regulator of primary production in

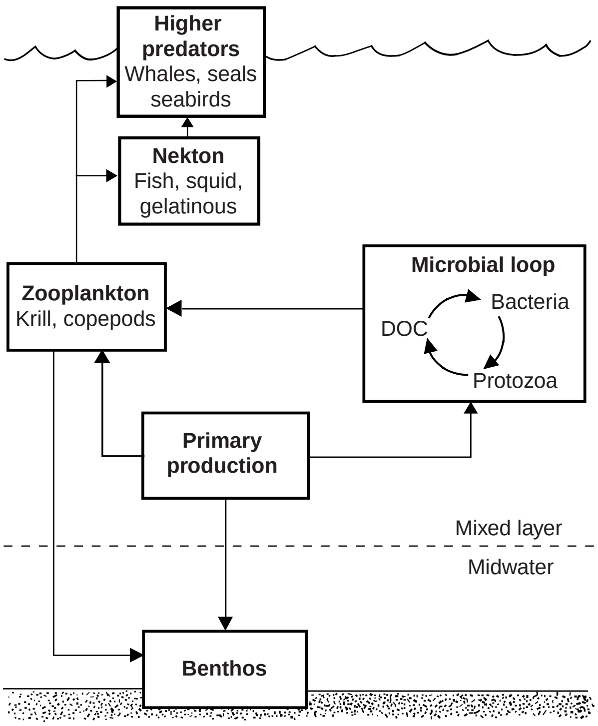

Figure 2 The basic structure of all marine food webs. Carbon fixed in primary production flows in three directions: to zooplankton herbivores (and thence to zooplanktonic and nektonic carnivores, and vertebrate higher predators), to the microbial loop, and via sedimentation to the benthos. In oceanic areas, the vertical flux of phytodetritus (from primary production) and particulate matter from zooplankton (primarily fecal pellets) passes out of the mixed layer and through the midwater to the benthos. In coastal areas, the benthos is within the mixed layer. Although specific food webs for individual oceanic locations will vary in complexity and the relative importance of different pathways, all have the same underlying structure. DOC, dissolved organic carbon.

the water column beneath. In particular where snow lies on the ice, surface incident radiation can be reduced to a sufficiently low level to prevent photosynthesis. The isolation of the water column from wind also reduces turbulence and many biological particles (both living and inanimate) sediment out of the photic zone.

Sea ice also has a positive effect on primary production in polar oceans. In areas where sea ice is melting (the marginal ice zone) the release of fresh water can lead to an area of increased water column stability that encourages rapid primary production. It is not at present clear to what extent the enhanced primary productivity is caused by the increased stability, by seeding by phytoplankton cells released from the ice, or by other oceanographic features; indeed, it is likely that each of these factors may be important in different places at different times.

A second important influence by sea ice is its role as a habitat, supporting a diverse microbial community in the interstices between ice crystals. This distinctive assemblage (sometimes called the sympagic or epontic community) can grow throughout annual sea ice but is almost always most highly developed at the interface between the ice and the underlying sea water. The growth of phytoplankton and other microbial primary producers can be so intense as to color the undersides of the ice deep green or brown, colors that are easily seen as floes are overturned by ships passing through ice in late winter or spring. The contribution of ice-associated primary production to production in the Arctic or Southern Oceans as a whole is not known with any certainty. Current estimates for the Southern Ocean are of the order of 25–30%.

In studies of sea ice communities much attention has been directed to diatoms, but the microbial community growing within ice can be rich and diverse. It includes bacteria and flagellates as primary producers and a variety of flagellates, ciliates, and other protozoans as consumers. Associated with these are a range of meiofauna, and the whole assemblage is grazed by consumers. Particularly noteworthy among these are amphipods (in both Arctic and Antarctic systems) and euphausiids (principally in the Antarctic, where sea ice plays an important role in the biology of the Antarctic krill, *Euphausia superba*). These herbivores are themselves subject to predation by specialist consumers associated with the undersides of ice, most notably gelatinous zooplankton such as ctenophores and in the Antarctic the cryopelagic fish *Pagothenia borchgrevinki*.

Primary Production and the Microbial Loop

The microbial loop (**Figure 2**) is known to be a feature of all ocean systems, though its importance varies from place to place. It is undoubtedly present in polar regions, and can be important at times. Summer chlorophyll biomass is, however, dominated by diatoms rather than the small cells that contribute directly to the microbial loop. Nevertheless, all the components of the microbial loop are well documented from polar oceans, and there is considerable release of dissolved organic matter from rapidly growing phytoplankton cells in summer. It is likely that the microbial loop is present and active in all polar seas, but that production is dominated by larger cells for much of the summer open water season.

One group of primary producers that are important in many oceanic areas, but that are absent from truly polar seas, are coccolithophorids. This may be because the low temperatures are unfavorable for calcification.

Short Linear Food Chains

The polar regions have long been famous for the presence of short, linear food chains. The classic example of this is the trophic relationship that characterizes the lower latitude regions of the Southern Oceans: diatoms–krill–whales. This is a three trophic level food chain through which energy progresses in just two steps from microscopic cells to the largest organisms the world has ever seen.

This particular food chain has long formed a paradigm for polar oceans in general (**Figure 3**). While there can be no doubt that in some places at some times energy flux through polar marine ecosystems can be dominated by such short, linear food chains, the system as a whole is more complex and nonlinear (**Figure 2**).

Vertical Flux

Vertical flux of biological material is usually measured by deploying sediment traps below the euphotic zone. Where this has been done on a year-round basis, vertical flux has been shown to be markedly seasonal. Almost all of the annual flux occurs in summer, and winter sedimentation rates can be almost nonexistent. Maximal rates appear to be associated with the ice edge, and swarms of zooplankton can produce a significant flux of fecal pellets.

Midwater

The midwater zone is one of the least explored in polar regions. It is known that many species characteristic of lower latitudes extend into polar regions, and this is probably because the oceanographic features that define the polar regions are typically surface features and their influence may not extend to the mesopelagic realm.

As with the midwater elsewhere, the food web in polar mesopelagic waters is characterized by crustaceans, fish, and gelatinous zooplankton. The latter are little known from polar regions because they are badly damaged by traditional net sampling techniques, and to date there have been no submersible expeditions to polar waters to complement those from temperate midwaters where gelatinous zooplankton have been shown to be very important.

Myctophid fish are a major component of the midwater fauna and they form an important link to the surface food web through their vertical migration. They rise into surface waters by night, and here they are both an important consumer of crustacean zooplankton and an important prey item for sea birds and other top predators.

Benthos

The benthos is an important component of the marine food web in all oceans. In shallow waters benthic organisms can feed directly within the zone of surface production, whereas in deeper waters they

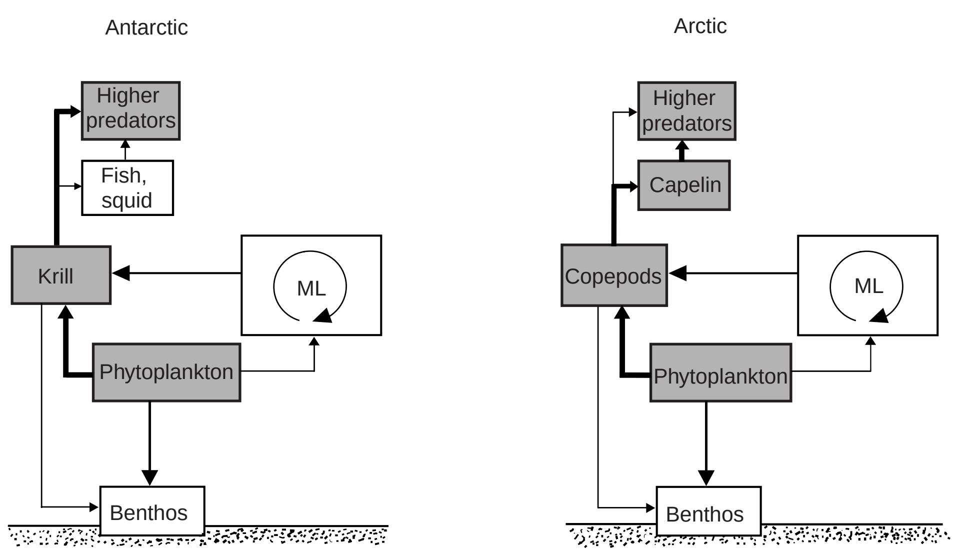

Figure 3 Representative polar food webs for the Antarctic (South Georgia) and the Arctic (Barents Sea), showing how energy flow can be dominated in some places at some times by a short, effectively linear, food chain. The major routes of energy flow are highlighted by the shaded boxes and the thicker arrows. The South Georgia example has become something of a paradigm for polar oceans in general. ML, microbial loop.

rely primarily on vertical flux from the euphotic zone.

In polar regions suspension feeders are particularly important, with sponges, ascidians (sea squirts), bryozoans, brachiopods, holothurians (sea cucumbers) and fan-worms all well represented.

Top Predators

Polar marine ecosystems have long been recognized as being rich in top predators (seabirds, seals, and whales). In the Arctic the important top predators are seabirds (especially alcids and gulls) and the smaller toothed wales, although in the past baleen whales were also important. In the Southern Ocean the important top predators are penguins, albatrosses, and petrels among the sea birds, and both toothed and baleen whales.

These top predators achieve greater biomass in polar regions than anywhere else in the world's oceans, and their role within the marine food web is very significant. Many feed directly on crustacean zooplankton, thereby creating the short linear food chains that can characterize the system at some times. Others feed on fish and squid, and in some polar regions the status of these top predators is being used as a simple measure expressing the overall integrated well-being of the polar marine ecosystem.

Seasonality

Two features contribute to the intense seasonality of the polar marine ecosystem. The first is that primary production, and hence food availability for herbivores, is constrained almost completely to the summer months. In consequence, the growth and reproduction of organisms at all higher levels in the food web (both plankton and benthic) is itself often constrained to summer. Many species, however, have life cycles longer than one year and must overcome the long winter period of food shortage. This they do either through the utilization of reserves, typically fat, laid down the previous summer (many zooplankton), or by utilizing general body tissue and 'de-growing' over winter (some zooplankton and many benthos).

This seasonality leads to very large differences in energy flux through the polar food web between summer and winter. There is also an important seasonal variation in food web structure in that many top predators migrate to low latitudes in winter, thereby decreasing predation pressure on lower levels of the food web.

Man and the Polar Food Web

Although the polar regions lie far from many home ports and can be extremely inhospitable, they have been subject to intense disturbance by man. The Arctic has long been a traditional fishing ground for both demersal and midwater fish, and at both poles a variety of top predators have been subject to intense exploitation. In neither the Arctic nor the Southern Ocean can the structure or dynamics of the marine ecosystem be regarded as pristine (in the sense of reflecting the position before the intervention of man).

In the Arctic three species of large whale have been either effectively eradicated or reduced to very low populations; several species of fish are now at levels that render them economically unviable; and a major benthic crustacean predator (Alaskan king crab) has been reduced to very low population levels. In the Antarctic the large baleen whales have been reduced to very low populations (though the smaller Minke whale may have increased as a result) and the Southern fur seal is recovering from the brink of extinction. Many demersal fish stocks have been reduced to very low levels, and intermediate levels of the food web (Antarctic krill) are now being fished.

We can only speculate as to the structure of these polar food webs prior to the intervention of man. The complexity of the system and the nonlinearity of many of the dynamical processes involved make both prediction and hindcasting almost impossible. It is distinctly possible, however, that following the disturbance of these systems, they have settled (or will eventually do so) to a new and different stable structure. We may never again have a Southern Ocean dominated by the great whales, no matter how long we wait. Such complexities also make it very difficult to predict the effect of further disturbances, such as the development of a new fishery, or climate change.

Although there are many general features common to both polar marine food webs, there are also features peculiar to each.

The Arctic Food Web

The Arctic is a deep-water basin surrounded by wide shallow continental shelves and almost completely enclosed by large land masses. Extensive river systems drain into the Arctic basin, delivering large volumes of fresh water and sediment. Exchange of water with lower latitudes is highly constrained, and most of the surface is covered with multiyear ice. The Arctic basin food web is probably relatively young, as it is likely that very little planktonic or benthic fauna was present at the height of the last glaciation.

Relatively little is known of the food web of the high Arctic basin as it is so difficult to work there. The benthos is low in diversity, though it is not clear to what extent this is a function of the relative youth of the system, the heavy input of fresh water and sediment in some areas, or the intense disturbance from bottom-feeding marine mammals. At lower latitudes there are important stocks of shoaling plankton-feeding fish, which have long been exploited by man.

The Southern Ocean Food Web

The Antarctic is in many ways a mirror image of the Arctic. It is a large continental land mass entirely surrounded by a deep ocean. The marine food web is likely to have been in existence for many millions of years, and while the zooplankton community appears to be relatively low in species richness, the benthos exhibits a diversity fully comparable with all but the richest habitats elsewhere.

The summer phytoplankton bloom is formed predominantly of the larger diatoms, and the haptophyte *Phaeocystis* appears not to be as important here as in the Arctic. The zooplankton is dominated by copepods and euphausiids, with *Euphausia superba* at lower latitudes and *E. crystallarophias* closer to the ice. Midwater planktivorous fish are almost absent, and the fish fauna is dominated by the radiation of two predominantly benthic/demersal groups: notothenioids on the continental shelf and lipariids in the deeper water of the continental slope. As with the Arctic, relatively little is known of the deep sea.

See also

Arctic Basin Circulation. Baleen Whales. Current Systems in the Southern Ocean. Fisheries and Climate. Marine Mammal Overview. Microbial Loops. Seabird Foraging Ecology. Southern Ocean Fisheries. Sperm Whales and Beaked Whales.

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POLICY

See **MARINE MAMMAL OVERVIEW**

POLLUTANTS

See **ATMOSPHERIC INPUT OF POLLUTANTS**

POLLUTION

Effects on Marine Communities

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Introduction

Natural communities of all types of marine organisms all over the world are being affected either directly or indirectly by pollution: directly by discharges of industrial and domestic wastes, offshore oil and gas drilling activities for example, and indirectly as a result of atmospheric pollution and global climate change. Some of these community changes are visually obvious in the field, such as the