Impacts of Global Warming on Polar Ecosystems

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2. ARE DECLINING ANTARCTIC KRILL STOCKS A RESULT OF GLOBAL WARMING OR OF THE DECIMATION OF THE WHALES?

by

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AFTER THE NEAR EXTINCTION of the stocks of great whales around Antarctica by the mid-1960s, krill biomass was expected to increase because of decreasing predation pressure. However, the opposite has apparently happened: krill stocks have declined by about 80% over the past three decades, accompanied by a concomitant increase in salp biomass. One explanation for the decline is that a stretch of sea ice off the tip of the Antarctic Peninsula, believed to be crucial to krill recruitment, has retreated as a result of global warming. If true, then the decline would have happened anyway and, if whale populations had not been exploited, they would now be undergoing severe starvation.

I propose an alternative hypothesis based on evolutionary ecology. In this view the exceptional "food chain of the giants" was maintained thanks to environmental conditioning by the giants, whereby the limiting element iron was recycled in the surface layer for longer by the feeding activity of the whales than in their absence. Since the whales were eating protein but accumulating lipids, they were sequestering energy and could well have been recycling essential elements, specifically iron, back to the ecosystem for phytoplankton to fix more energy. Such a "manuring mechanism" by the giants would have increased the spatial extent of the productive region. In their absence, productivity based on recycled iron has gone down, the productive area has shrunk and salps have moved in. The current trend urgently requires action if we wish to ensure the recovery of Antarctic whale populations from the brink of extinction where they are still hovering.

The iron recycling hypothesis is presented in this essay and can be tested in large-scale, long-term iron fertilisation experiments in the south-western Atlantic where most of the krill population was formerly located. Apart from

◄ **Photo 2.1: Humpback whale (*Megaptera novaeangliae*)**. These cetaceans, avid consumers of krill, migrate thousands of kilometres from their breeding grounds in the tropical seas to the waters of Antarctica where they feed during the southern summer.

furthering our understanding of pelagic ecosystem functioning, an added benefit of these experiments would be to test the feasibility of larger-scale iron fertilisation to sequester significant quantities of atmospheric CO_2.

2.1. INTRODUCTION

In the 1920s, at the height of the Antarctic "whale rush", when 20,000 great whales were being converted every year into soap, candles and dog food, some far-sighted British scientists and policy makers realised that, without proper management, the bonanza would soon end in disaster (Hardy 1967). History proved them right, and the whale populations were depleted almost to extinction within a few decades. By the end of the 1930s, about 300,000 Antarctic blue whales had been killed (figure 2.1), and the population was further reduced to about 360 individuals by the time the moratorium on whaling was agreed upon in 1964. In 1996, their population size was estimated at 1,700, and it is reported to be increasing (Branch et al. 2004). However, future prospects for the recovery of the Antarctic blue whale—the largest animal that has ever inhabited our planet—are not that bright.

Antarctic blue whales feed on a single species of pelagic crustacean, the Antarctic krill (*Euphausia superba*), and the annual food requirements of the

Figure 2.1: Whale catches in Southern Ocean waters from 1904 to 1981
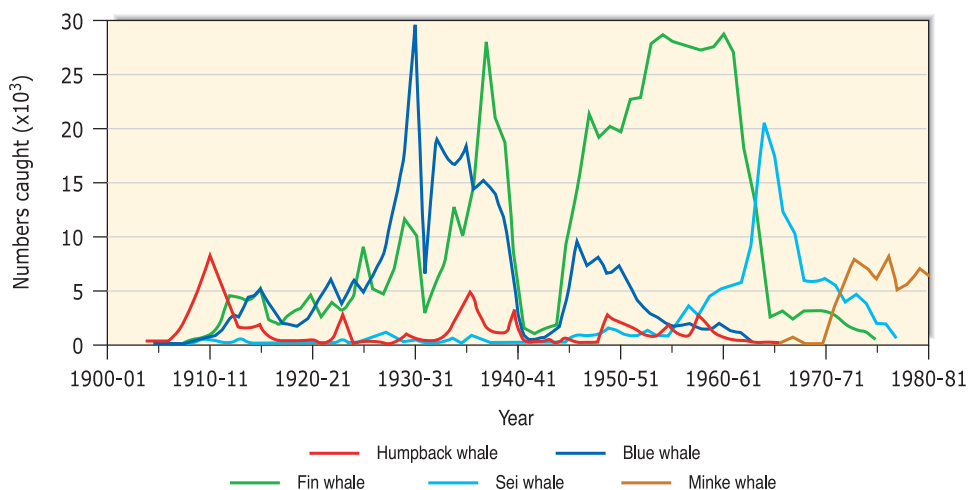
Including data from land stations, moored factory ships and pelagic catches, though the numbers only represent whales landed.

Source: Laws 1977; Knox 1994.

Photo 2.2: Krill (*Euphasia superba*). This crustacean is among the most abundant marine animals and forms the base of the food chain in the Southern Ocean.

intact whale stock has been estimated at 190 million tonnes (Laws 1977). The magnitude of this figure can only be comprehended by comparing it with others in the same range: the biomass of the blue whale stock prior to whaling was about 40 million tonnes, which is about as much as the biomass of one billion humans, i.e., one-sixth of the current human population. Further, the annual global fish catch since the 1970s is equivalent to less than half the biomass of Antarctic krill that was annually eaten by the whales prior to whaling, and in less than 1% of their distribution area. But while the fish harvest has resulted in serious global depletion of stocks, the krill catch by whales was evidently sustainable. Clearly, the "food chain of the giants" (diatoms-krill-whales) was highly efficient; its resilience demonstrated by survival through past climate cycles. So how was the food supply of the whales maintained?

The greatest advance in understanding of the factors that control ocean productivity in recent decades has been proof of the limiting role of iron. What used to be known as the Antarctic Paradox—low productivity in a sea of nitrate—was later recognised as characteristic for the equatorial and sub-Arctic Pacific as well and termed the high nutrient, low-chlorophyll

(HNLC) condition. Evidence for iron limitation of phytoplankton growth rates in all three regions of the world ocean, otherwise widely differing in their physical, chemical and biological properties, has now resolved the issue. To my mind, incorporating this new knowledge into the current conceptual framework of Southern Ocean pelagic ecosystem structure and functioning is tantamount to a paradigm shift. In the following sections, I briefly outline the history of the concept of iron limitation of productivity in the Southern Ocean before proceeding to the real Antarctic paradox—the presence of remarkably large animal stocks in a moderately productive stretch of ocean.

2.2. IRON LIMITATION OF PRODUCTIVITY

T. J. Hart, one of the scientists who participated in the HMS *Discovery* cruises and worked up the phytoplankton samples, was struck by the high phytoplankton biomass in the waters between South Georgia and the Antarctic Peninsula as compared to other, equally nutrient-rich water masses elsewhere around Antarctica. He observed that productivity was higher in the proximity of land masses when compared to the open ocean and speculated that trace elements such as iron and manganese washed off from the land and sediments could be one of the factors responsible (Hart 1942). At that time, trace metals could not be accurately measured because of contamination problems, so their possible role remained in the realm of speculation. Indeed, it was not until the late 1980s that the first reliable estimates of iron concentrations in sea water were made by the group headed by John Martin. They found over ten times higher iron concentrations in near-shore waters compared to the open ocean (Martin 1990). Also, their low values were much lower than previous estimates.

Martin and his co-workers also added iron to natural sea water in bottles treated with ultra-clean techniques and showed a strong growth response by phytoplankton in comparison to control bottles. Such experiments had been carried out before, but growth had occurred in all bottles and was attributed to a mysterious "bottle effect". Martin attributed the lack of an effect in earlier experiments to contamination of the control bottles (in the human environment, iron is everywhere), so the real achievement of his group was to demonstrate the lack of an effect in the controls. This was achieved by employing painstakingly decontaminated, ultra-clean sampling gear, as well as bottles and reagents, and was the first real evidence that trace quantities

of the essential element iron were needed to stimulate phytoplankton productivity. However, this was insufficient proof that the nutrient-rich waters surrounding Antarctica were poor in phytoplankton because of iron limitation. Light limitation due to deep mixing and heavy grazing pressure by large zooplankton stocks were the alternative explanations for the "Antarctic Paradox" of low productivity despite high nutrient concentrations. The role of these factors, particularly the effect of grazing, could only be tested in situ.

Since the mid-nineties, a total of nine open-ocean iron fertilisation experiments carried out in land-remote north and equatorial Pacific as well as Southern Ocean waters have demonstrated unambiguously that the supply of iron limits phytoplankton growth in these nutrient-rich waters (Boyd et al. 2007). Another of their conclusions was that neither poor light availability due to deep mixed layers nor heavy grazing pressure exerted by small and medium-sized zooplankton hindered the development of diatom blooms. Whereas the biogeochemical significance of these experiments in the framework of climate research is acknowledged, their implications for our understanding of how pelagic ecosystems, particularly their higher trophic levels, deal with iron limitation or its alleviation has not yet been explored. In particular, the higher productivity around the continent and islands evident from satellite images (map 2.1) can now be attributed, with greater confidence than before, to the supply of iron from land masses, including runoff and contact with sediments.

It follows that iron input from upwelling deep water along the Antarctic Divergence is comparatively minor, as can be clearly seen from satellite images of chlorophyll seasonality in the Southern Ocean (map 2.1). Indeed, the southern branch of the Antarctic Circumpolar Current (ACC), which receives the northward moving, upwelling deep water, reflected in its high silicic acid concentrations, is evidently the most barren in the entire Southern Ocean. In striking contrast, productivity along the convergent Antarctic Polar Front (APF), characterised by downwelling and mixing of Antarctic Zone water with warmer water from the northern ACC, tends to be conspicuously higher. However, higher productivity along the APF is not a universal feature, but is restricted to stretches south of the three adjoining continents, which strongly suggests local input of iron, most likely due to settling out of dust mediated by rainfall. As a result of iron limitation, the bulk of the nitrate and phosphate nutrients upwelling along the southern boundary of the ACC and subsequently circulating within it are returned

Map 2.1: Chlorophyll distribution in the Southern Ocean
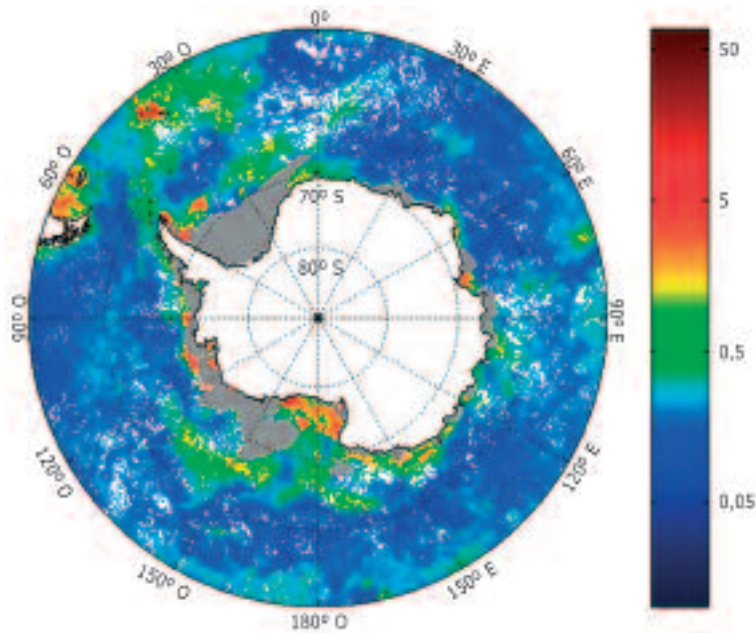
Composite satellite image of chlorophyll concentrations, a measure of productivity, in the Southern Ocean, recorded by the SEAWifS satellite. Our thanks to the SEAWifS project and the Distributed Archives Centre of the Goddard Space Flight Centre for the production and distribution of these data. Activities sponsored by the Mission to Planet Earth programme of the NASA. Thanks also go to B. Raymond and J. Schwarz for the creation of the map. Colour scale in mg of chlorophyll per m3

Source: Smetacek and Nicol. Reproduced by permission of Macmillan Publishers Ltd: *Nature,* vol. 437/15, September 2005, © 2005.

largely unused to the deep ocean as Antarctic Intermediate Water along the northern boundary of the ACC. In contrast, silicic acid is extracted and retained within the ACC and its underlying sediments. This discrepancy between Si on the one hand and N and P, hence also C, on the other, has been dealt with elsewhere (Smetacek et al. 2004). The point here is that the residence time of iron in the sea must be much shorter than that of all other biogenic elements including Si. However, the factors influencing the eventual fate of iron are still under study, so some educated speculation based on consideration of what is currently known, and can be considered fact, is warranted to guide future research.

The seaward extent of the gradients between the narrow productive margins and the barren open seas are determined by two independent factors: the

rate of dilution with iron-limited waters and the efficiency of uptake and retention of iron by the biota in the surface layer. Inorganic iron compounds are highly insoluble in oxygenated, alkaline sea water (saturation values range from around 0.2 to 0.5 nanomoles per litre). However, iron is biochemically highly reactive and is bound by a variety of organic compounds called ligands; in some cases so tightly as to be inaccessible to bacteria. Interestingly, strong iron-binding compounds known as siderophores are deployed by our bodies in saliva and plasma to limit the growth of bacteria in our mouths and blood. The bacteria that do manage to invade are grazed by white blood corpuscles. So it is not only the oceans that are iron- and grazer-limited. Given the trace amounts of iron (around 2 nanomoles per litre) required to achieve phytoplankton growth to bloom status (over 2 mg of chlorophyll per m^3), one can envision highly complex, species-specific interaction between biota and their potential iron supply. We shall return to the ecological impact of iron later following a brief overview of the trophic structure of the ecosystem.

2.3. DIATOMS, EUPHAUSIIDS AND BLUE WHALES

2.3.1. Diatoms

Phytoplankton blooms occur when iron-replete, nutrient-rich waters experience adequate light levels, such as in spring or in upwelling regions of high and low latitudes respectively. These blooms are invariably dominated by diatoms belonging to comparatively few genera of which *Chaetoceros* and *Thalassiosira* are particularly widespread. Colonies of the flagellate genus *Phaeocystis* can also contribute substantially to bloom biomass in some regions. The spring phytoplankton blooms of the land-near Southern Ocean are not exceptional in either composition or behaviour compared to those of other regions. Mass sinking in their aftermath is commonly observed, however, and this is not triggered, as in other regions, by macronutrient exhaustion. It is therefore logical to assume that the decline phase in Antarctic waters is triggered by iron exhaustion, although this has yet to be proven. The diatom species typical of iron-rich coastal regions differ from those of ice-free, land-remote Antarctic Circumpolar Current (ACC) species, which tend to be large, heavily silicified or equipped with long, barbed spines that appear to have evolved as deterrents against grazing by smaller ingestors such as protists and smaller copepods (Smetacek, Assmy and Henjes 2004).
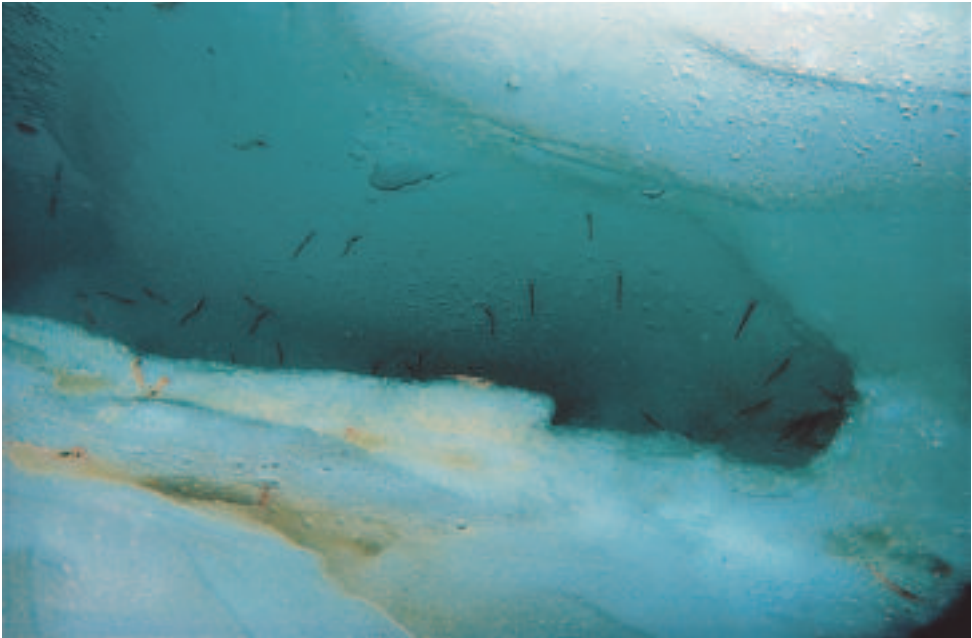
**Photo 2.3: Krill feeding on ice algae from the undersurface of sea ice**

In ice-covered regions, melting of the ice cover is a precondition for bloom development. However, blooms only occur in the presence of sufficient iron, which explains their absence along the retreating ice edge around most of Antarctica. The sea ice itself is also colonised by ice algae, which can reach high concentrations, albeit in narrow layers. Their distribution is highly patchy across scales of tens to hundreds of metres. Hence, although eye-catching, their contribution to water column productivity is relatively minor. Nevertheless, the sea-ice cover provides a source of concentrated food to zooplankton, like copepods, amphipods and krill, that are capable of feeding on them by scraping the ice. In the Antarctic, krill clearly dominates the zooplankton community adapted to life on the underside of sea ice (photo 2.3). However, there are marked regional differences. Thus, although a systematic comparison has not yet been made, it appears that krill stocks in the Weddell Sea, particularly along its northwestern boundary, are much larger than in the Ross Sea. This might be the reason why blooms of *Phaeo-cystis*, which are easily eaten by euphausiids as compared to copepods, are regular and extensive occurrences along the Ross Sea ice edge, but not that of the Weddell Sea (Smetacek, Assmy and Henjes 2004).

2.3.2. Antarctic krill

Krill belong to the euphausiids, a group of zooplanktonic crustaceans that occupy the size class above the copepods and range in size from 1 to 6 cm. Although not related to them, they resemble the more familiar shrimps in body shape, because their mode of fleeing predators is the same: rapid flips of the strong tail muscles. The diet of the different species varies from filtering the water for the indiscriminate collection of unicellular plankton down to about 10 µm size to capturing motile prey such as copepods. The distribution patterns of the different species mirror oceanographic provinces characterised by temperature. Krill occupy the penultimate temperature range and tend to be concentrated, like euphausiids elsewhere, along the shelf break. The slightly smaller *Euphausia crystallorophias* occupies the coldest strip of water along the deep continental shelves bordered by the Antarctic ice cap.

Krill differ from other euphausiids in their greater size (up to 6 cm), longevity (over 6 years) and flexibility in behaviour: they are equally adept at surviving in the open water column as they are in the rugged undersurface of pack ice. They also feed on the entire range of food accessible to euphausiids in general—from filter-feeding on small-celled plankton to capturing larger copepods (figure 2.2). Another feature of krill feeding behaviour that

Figure 2.2: Krill, its major food (diatoms and copepods) and predators (birds, seals and whales) against the backdrop of its preferred habitat
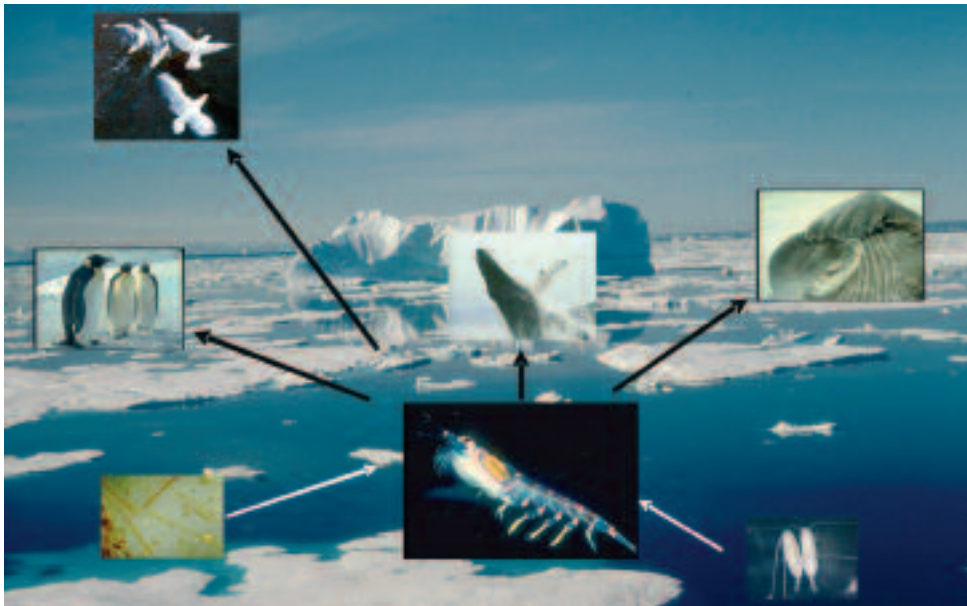
they share with many other zooplankton taxa, including copepods, is what from our perspective can only be labelled as gluttony: the tendency to ingest far more food than can possibly be digested. This "superfluous feeding" behaviour of krill (Clarke et al. 1988) is illustrated by the individual depicted in photo 2.4. It has collected a large amount of food in its feeding basket which it proceeds to ingest, egesting a continuous faecal string that extends from its tail-end, makes a loop not seen in the photograph and enters the food bolus of the same individual. The adaptive significance of voracity for pelagic copepods has been attributed to environmental "gardening": adults convert a greater proportion of the diatom bloom into faeces that are subsequently recycled by the microbial network and made available to larval stages (Smetacek 1985). In the absence of this retention behaviour (Peinert et al. 1989), a greater proportion of the diatom biomass would sink out, and impoverishment of the surface layer would be more severe, resulting in lower recruitment of the grazers. In the case of krill, an analogous explanation would be the environmental conditioning of the entire habitat, as expanded upon below.

Unlike related species of euphausiids, krill have not been observed to lay down lipid depots in winter in the form of wax esters. Their fat reserves are

Photo 2.4: Two individuals of krill in an aquarium feeding on a dense culture of aggregated ice-algal diatoms. Their voracity is reflected in the size of the food bolus and the continuity of the ingested food and faeces emanating from the tail end of the animal in the foreground.

in the form of readily accessible triglycerides that do not seem to be concentrated in special depots evolved for the purpose (lipid sacs). Nevertheless, these lipids can constitute a significant percentage of body weight (Hagen, Van Vleet and Kattner 1996) in the same proportion as wax esters in species with specialised depots. Krill can also starve for over a year and shrink in body size, presumably after lipid reserves have been used up. The point is that krill are active throughout the year and do not undergo any form of dormancy, which is surprising given the strong seasonality undergone by the winter sea-ice covered environment they occupy.

If krill are starved together in aquaria, they will capture and eat their neighbours. This common observation tends to be downplayed as an artefact of captivity. How widespread cannibalism is in the wild is not known, but it has certainly been observed (Hamner and Hamner 2000). To my mind, it appears unlikely that the complex behaviour necessary for the tasks involved—decision-making, capturing, killing, dismembering and eating one's neighbour—can be learned de novo in the aquarium. That adult krill prey on their larvae is not disputed. Indeed this behaviour is invoked to explain the segregation of adult and juvenile populations. Cannibalism is of interest when considering its ecological and evolutionary implications, as it will enable self-regulation of population size to the food supply, particularly under the ice cover, and select for those individuals practising it. In open water, on the other hand, krill live in tight, fish-like schools that protect individuals against attacking predators (Hamner and Hamner 2000). This safety-in-numbers response implies that individual fitness increases with the size of the population in open water, but not necessarily under the ice, where individual krill seek safety within the recesses of the ice cover (personal observation). Krill aggregations under the ice can form schools and escape in the open water. It is tempting to suggest that environment-switching behaviour patterns evolved by krill enable it to optimally gear population size to the food supply in the sea-ice zone around Antarctica. The properties of krill indicate that it has evolved as a space holder, capable of channelling a substantial proportion of available resources into population biomass.

Unlike salps, which reproduce by budding new individuals on a colony stalk and hence have biomass doubling rates of hours to days, depending on temperature, krill have evolved life cycles in which growth from egg to adult takes well over a year. Krill recruitment is dependent on a combination of adequate food supply and protection from predators in the sea-ice

habitat. The gonads of adult krill disappear in winter and only develop when sufficient food is available. Eggs are laid off the continental slope (above 1,000 m depth) where they sink to around 1,000 m depth before hatching. This strategy reduces mortality by predators that live in the surface layer. Larval development occurs on the way up without feeding. First-feeding larvae require high food concentrations and cannot arrest development, i.e., they are reported to starve to death, unlike adults. Larvae are believed to survive best along the melting ice edge, which is rich in ice biota but where they also find shelter from predators under ice floes. However, larvae also occur in open water away from sea ice, so its presence is not obligatory.

In sum, the biology of Antarctic krill (*Euphausia superba*) is unique in many ways: krill exploit an exceptionally broad range of food resources: nano- and microplankton, particularly diatoms, but also zooplankton, particularly copepods. And captive krill, as stated, are even cannibalistic. Krill feed prodigiously when food is plentiful, but can starve for many months. They do not hibernate, but can store substantial lipid reserves and also shrink in size when starved. Krill inhabit sea ice or the open ocean equally well, as dispersed individuals or in tight schools that can swim long distances (up to 30 km/day), enabling them to adequately exploit a patchy food supply. Their population size is much larger than that of any other euphausiid: a century ago, their biomass will have been substantially higher than the current global human biomass (about 250 million tonnes). So krill occupy a broader niche than either zooplankton or planktivorous fish.

2.3.3. Blue whales

Blue whales can weigh as much as 150 tonnes and are the largest animals that ever inhabited the earth. It bears mention that they feed almost exclusively on euphausiids throughout their range. Regional populations occur in all the oceans, but the Antarctic blue whale was the largest, both in terms of individual and population size, prior to the invention of harpoons that exploded inside the animals thus preventing cadavers from sinking. Life cycle stages in blue whales are remarkably short in comparison to their large size—in the same range as cattle and about three times shorter than elephants (and humans). Scientists of the *Discovery* era estimated that adult size and sexual maturity were attained about three years after birth and that life span was about 25 years (Hardy 1967). However, the latter figure is probably a guess,

Photo 2.5: Blue whale (*Balaenoptera musculus*). This cetacean is the largest animals ever to have lived on the planet and a major consumer of krill.

whereas the former was derived from dead whales examined in a whaling station in South Africa (Hardy 1967). Suckling a calf that doubles in size in a single season will require a Herculean effort on the part of the mother, as she must eat more than twice as much as non-suckling whales. Since growing individuals are most susceptible to food shortages, recruitment will depend on adult mortality, which, given the lack of predators, will be in old age. Further indications that recruitment was tightly geared to prey availability, i.e., that population size was located at the upper end of the system carrying capacity, are provided, firstly, by the absence of territorial behaviour, implying that suckling females will be competing with other non-suckling individuals, and, secondly, by the larger size of females compared to males, implying that feeding efficiency increases with size.

Of course, blue whales would have competed with other baleen whales, particularly fin whales, which are significantly smaller, at 50-80 tonnes, but have the same muscular, streamlined body shape. However, they feed on a broader range of prey items, including amphipods and fish. The Antarctic population, which was considerably larger than that of the blue whale, was located further to the north, albeit with considerable overlap. Given the paucity of other food

sources, krill must have constituted a significant proportion of their diet. Smaller krill predators such as seals and penguins together constituted less than a tenth of the biomass of the baleen whales, so are not likely to have been serious food competitors.

2.4. DISTRIBUTION OF *EUPHASIA SUPERBA*

The first systematic survey of krill distribution in the Southern Ocean was carried out by the cruises of HMS *Discovery* in the 1920s and 1930s. By that time, large-scale whaling was in full swing and it came as no surprise that the region with the highest densities of krill coincided with that of their main predators, baleen whales. This region, known as the Antarctic Peninsula Plume (APP), is located in the southwest Atlantic and extends from the Antarctic Peninsula (62°S) to South Georgia (53°S) including the South Shetland and Orkney Islands. To the southeast it is bounded by the northern extent of summer sea ice in the Weddell Sea, and to the northeast approximately by the Antarctic Polar Front (APF) up to the latitude of South Georgia. To the east, it extends as far as the South Sandwich Island arc (30°W). The maximum area of the APP is approximately 2 million km².

Net catches with fine-meshed nets in this region also collected the highest concentrations of phytoplankton recorded anywhere in Antarctic waters. Clearly, high krill densities were supported by the high productivity of this region, but the reasons for the latter were not clear at the time. This region is a zone where different water masses, and hence the krill populations living in them, mix with one another. Eastward flowing waters from the ACC to the north, and from the northern rim of the Weddell Gyre to the south, mix with water from the Bransfield Strait in the middle along the Weddell-Scotia Confluence. All these water masses are rich in the macronutrients nitrate, phosphate and silicic acid, but the property they have in common, and in which they differ from their source waters outside this zone, is that they have had contact with land masses: the ACC water with the northwestern and the Weddell Sea water with the southeastern coasts, islands and shelves of the convoluted Antarctic Peninsula. Elsewhere around Antarctica, the northern distribution of *E. superba* coincides with the extent of winter sea ice, but the only region where this rule does not hold is the northern half of the APP, where large krill stocks and their accompanying predators extend all the way across a 1,500 km stretch of open ocean to South Georgia and beyond.

Clearly, the Peninsula with its many islands is the richest source of iron in Antarctica, but this does not explain the downstream extent of its effects. One would expect local diatom blooms in coastal waters that would quickly use up the iron and sink it down to the benthos, as usually happens in northern temperate and Arctic seas. Instead, high productivity is maintained across the widening APP from the Weddell-Scotia Confluence to the side of the triangle between South Georgia and the continent. The oceanward extent of this high productive water is remarkable and cannot be explained by physico-chemical processes of iron supply and transport alone. A more efficient recycling of iron needs to be invoked, such that a given atom of iron has a longer lifetime in the surface layer. This can be achieved if predators contribute to retaining iron by deploying larger amounts of iron-complexing compounds (ligands) than elsewhere. Such an iron-recycling ecosystem, in which blooms are grazed down by roving schools of mobile herbivores (krill) that release and maintain the iron inventory in the surface layer, would contrast with the iron-sinking ecosystem dominated by coastal diatoms with a boom-and-bust life cycle (Smetacek et. al. 2004). In the latter case, ungrazed diatom cells and phytodetritus sink out *en masse* in the aftermath of blooms. The iron triggering the bloom is lost with sinking particles weeks after being incorporated into algal biomass. The spatial extent of productive coastal waters is accordingly curtailed. A conceptual framework of the possible fitness advantages accruing to the key players in iron-retaining ecosystems as compared to iron-sinking ones needs to be developed. We will return to the question of self-maintaining control mechanisms amongst the biota after a quantitative assessment of the diatom-krill-whale food chain.

2.5. KRILL STOCK SIZE

Estimating the stock size of krill from direct measurements is a challenge, because it occurs across a broad range of distribution patterns; from tight schools with a very high density of individuals to a few individuals scattered over large areas. Its depth preferences are also not as predictable as those of smaller zooplankton, i.e., a clear diel cycle is not evident. Further, it can hide under ice cover over a significant portion of the year, and krill densities under summer sea ice cover are not known. Hence krill stock size estimated from net catches and acoustic surveys and extrapolated over the known krill areas range between 80 and 1,000 million tonnes (Everson et al. 1990; Nicol et al. 2000).

An alternative means of estimating krill biomass is by assessing that of their various predators, particularly the baleen whales for which reliable numbers exist because of whaling records. Nevertheless, these figures are conservative because they do not include harpooned whales that were not landed but subsequently died. According to industrial whaling records of the past century, about 2.7 million great whales were killed globally, of which the majority were taken in the Southern Ocean. Of these, 300,000 Antarctic blue whales were killed in the Atlantic sector during the 1920s and 30s (figure 2.1). This is too short a time for recruitment to have had a significant effect, so this figure represents a conservative estimate of the actual population size. Some 490,000 fin whales were killed but over a longer period. From figure 2.1, we can derive a minimum size of the krill-dependent whale population prior to whaling of 500,000 individuals. Assuming average weights of 100 and 70 tonnes for blue and fin whales respectively, and including also the krill-feeding humpback whale (of which 130,000 were killed), their combined biomass must have amounted to at least 50 million tonnes. A round figure has been deliberately chosen to emphasise the tentativeness of this number.

So what is the minimum food requirement of this whale biomass? The great whales are reported to have spent about three months in the Southern Ocean feeding and the rest of the year lolling about in warmer waters of lower latitudes. They arrived in their feeding grounds in lean shape and put on enough blubber in three months to tide them over the non-feeding nine months. Employing the textbook transfer efficiency between trophic levels of 10:1, these three whale species will have eaten 500 million tonnes of krill annually. Continuing this line of argument, the size of the krill stock providing this amount of food each year will have been at least three times this figure, i.e., 1.5 billion tonnes. As we shall see below, this stock size is too large to be accommodated by the Southern Ocean ecosystem based on textbook trophic level transfer efficiencies of 10:1. So the whales must have eaten less. But how much less?

Laws (1977) assumed that the great whales ate 3% of their body weight per day during these three months and estimated their food demand at 190 million tonnes of krill annually. This amount came to be known as the "krill surplus", as it should have been available to other krill predators such as minke whales, seals and penguins after the demise of the whales. However, little evidence for this surplus, manifest in an explosion in numbers of smaller krill predators, has been reported, although it has been searched for. So the whales must have

Photo 2.6: Humpback whale in tropical waters during its breeding season. Like other large whales, the humpback only feeds during its three-month sojourn in Antarctic waters, where it fattens thanks to its huge intake of krill. It then lives off the stored fat as it journeys to its breeding grounds in warmer, more northern waters.

eaten even less, perhaps just 1-2 % of body weight in the three-month feeding season, as suggested by Mori and Butterworth (2006). However, the problem of the missing krill surplus cannot be dismissed by denying the whales their food, as a simple calculation shows.

There are no data to directly assess the food requirements of the great whales. Comparisons with wild land animals are inappropriate, because aquatic animals do not have to work against the gravitational field by carrying their weight around. So their energy demands, even for long migrations, will be much less, although they do have to overcome the viscosity of the medium. Comparison with domestic animals fed with high quality food and kept in confined spaces are more appropriate. Thus, pigs convert about 30% of the ingested food into biomass, the theoretical upper limit being about 50%. Assuming that the difference in weight of whales arriving and departing from the feeding grounds amounted to about 25-30% of body weight, which is a realistic range, their minimum food requirement just to reach this figure will have been 1% of body weight over a 100-day period. Since the blue and fin whales are muscular animals actively seeking and capturing their

prey, their food conversion factor over an annual cycle can hardly have been in the same range as that of stall-fed pigs. Besides, pregnant and suckling females will have had to eat twice or more the amount eaten by males. So even 3% of body weight will not have sufficed in their case. The point of this exercise is that Laws (1977) figure of 190 million tonnes of krill annually consumed by predators, of which 150 were due to whales, is actually a conservative number. The biomass of the parent stock recruiting the former figure will have been about 600 million tonnes, given that krill require about two years from egg to egg.

The area covered by winter sea ice around Antarctica is 20 million km², so the average biomass of krill in its habitat will have been 30 g per m², equivalent to 3 g carbon/m². Adult krill weigh about 1 g, so there will have been an average of 30 krill per m². Again, employing the standard textbook transfer efficiency of 10:1 between trophic levels, the annual food demand of this krill population will have been 30 g carbon/m². If we convert this figure to the amount of nitrate taken up by phytoplankton eaten by krill, we arrive at 10 millimoles nitrate/m³ in a 50 m deep surface layer. Nitrate concentrations in the Southern Ocean at the beginning of the growth season are 30 millimoles/m³, so the above figure is feasible but implausible for a number of reasons: the krill population is concentrated in restricted areas; the food demand of other grazers has been ignored; and conservative estimates have been used all along. But we know that the bulk of the krill population (50%) was concentrated in the APP, which has a maximum area of 2 million km², including the area north of the winter sea-ice cover. Based on this area and the krill stock size of 600 million tonnes estimated above, the standing stock of krill in the APP will have been 150 g krill/m² or 15 g carbon/m²—about twice the biomass of an average phytoplankton bloom. Clearly the textbook trophic transfer efficiencies of 10:1 cannot apply to the diatom-krill-whale food chain. The "food chain of the giants", in other words, must have been much more efficient.

So why has this problem not received the attention it deserves, given the basic calculations from which it has been derived? The main reason is a drifting apart of the scientific communities concerned with phytoplankton productivity, on the one hand, and population dynamics of fauna and their food base, krill, on the other. Previously, the plankton biology community had justified its research by reference to the need to quantify the food base of top predators, but in the past decades attention shifted to the role of the Southern Ocean in regulating atmospheric CO_2, within the framework of the interna-

tional Joint Global Ocean Flux Study (JGOFS). Since most of the work was carried out in the open ocean, the role of top predators could be conveniently ignored. Meantime, scientists studying vertebrates are organised in the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) under the umbrella of SCAR (Scientific Committee on Antarctic Research). Since animal populations have shrunk so much, food limitation does not seem to be the problem any longer, except in special cases such as where access to the sea is blocked by icebergs.

An attempt to quantify the contribution of air-breathing predators to the ocean's CO_2 balance (Huntley et al. 1991) was scoffed at by those who used the size of current stocks to downplay the significance of air-breathing krill predators on air-sea exchange of CO_2. The arguments against a significant role of these predators are biased by what Pauly (1995) called the shifting baseline syndrome, according to which each generation of fisheries biologist takes as the baseline the stock size which prevailed at the time when the respective scientist began his or her career. As we have seen in the calculation above, stocks of air-breathing predators were orders of magnitude larger before their decimation by humans. Similarly, a study carried out by Priddle et al. (1998) in

Photo 2.7: Adélie penguins (*Pygoscelis adeliae*). Adélies feed almost exclusively on krill and are among the penguins most exposed to the impact of global warming.

which krill biomass was related to that of their predators, on the one hand, and their phytoplankton food supply on the other, found that the budgets balanced nicely on both sides. However, the predator stock size considered was only a fraction of that prevailing at the time of the great whales. So productivity must also have been much higher, in other words it must have gone down since the demise of the whales.

After the demise of the whales, krill biomass and that of their remaining predators—minke whales, seals and penguins—were expected to increase in the APP. Indeed there is some evidence that the other predators did respond initially, suggesting that they were food-limited. However, the effect lasted only until the 1970s and has since apparently reversed (Mori and Butterworth 2006). Contrary to the expectation that krill biomass would increase following decimation of their major predators, resulting in a "krill surplus", evidence is mounting that krill biomass has undergone a drastic decline over the past few decades.

2.6. EVIDENCE FOR THE DECLINE OF KRILL BIOMASS

Evidence for the decline of krill biomass can be gathered from several sources, but the magnitude and reasons are under debate. Comparisons of visual observations of krill swarms from ship decks throughout the Southern Ocean, particularly between pre-World War II and current eras, clearly indicate that krill swarms are no longer sighted as often as they used to be (E. Pakhomov, personal communication). It has been suggested that the decline in sightings of surface krill is due to a change in krill behaviour: schooling krill now stay at greater depths than they used to. The reasons for this change in behaviour and how it could have been modified by natural selection over such a short interval is hard to explain. Decline in total stock size is a more parsimonious explanation.

It has been suggested that a krill surplus did not develop, because the krill continued to be eaten by growing numbers of other predators like minke whales, seals and penguins. This explanation is unlikely because their population biomasses are nowhere near those of the great whales. The biomass of one blue whale is equivalent to 250 crabeater seals or 30,000 Adélie penguins! Given that the food consumption per body mass of whales will be lower than that of seals and penguins, there would still be a huge discrepancy between the food demand of the great whales and that of all other krill predators combined. So it is highly unlikely that predation pressure alone could be responsible for

ongoing krill decline. This also applies to the krill taken by current fisheries (Mori and Butterworth 2006).

The most compelling evidence for the decline (figure 2.3) has come from a recent statistical assessment of all scientific krill net catches carried out since the *Discovery* era, which indicates a drastic reduction in krill biomass of around 80% in the APP, above all in the last 30 years (Atkinson et al. 2004). The same study showed that, in contrast, the biomass of salps has increased in the same area. The salp range has been clearly moving southwards in the last 50 years particularly in the Indian and Pacific Sectors. Loeb et al (1997) have argued that salps prefer the permanently open waters of the ACC, whereas krill are more partial to the seasonally sea-ice covered zone further south. Since the sea-ice extent has retreated recently only in the APP region, the circumpolar southward increase in salp occurrence cannot be explained by sea-ice cover. Indeed, as demonstrated by the large krill populations around ice-free South Georgia, productivity expressed in phytoplankton biomass is a more likely determinant of krill vs. salp dominance than the presence or absence of seasonal sea ice. Open-ocean salps are reported to choke at phytoplankton concentrations typical for shelf waters.

Figure 2.3: Decline in krill stocks in the SW Atlantic from 1976 to 2003
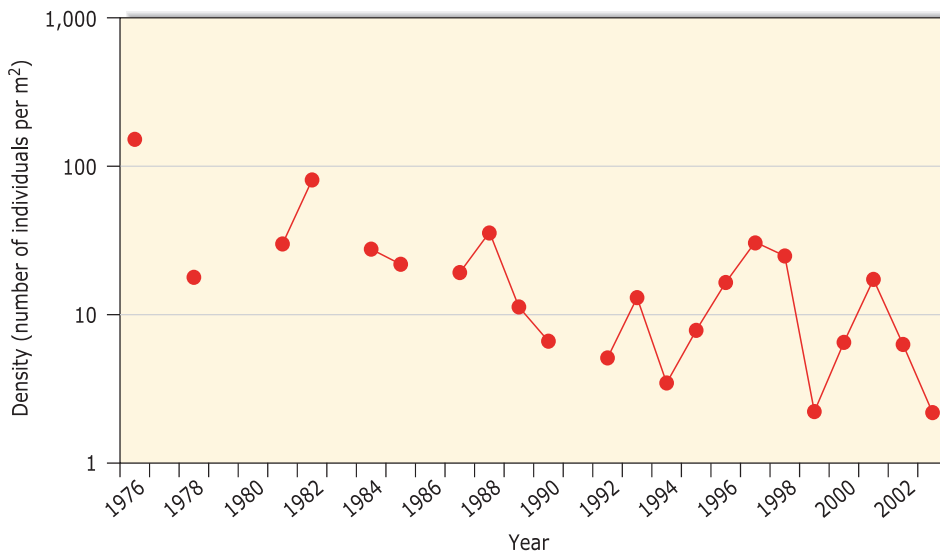
Krill density based on data from 4,984 stations.

Source: Atkinson et al. 2004.

Since salps are more abundant in open-ocean, iron-limited areas than in the high-productive regions favoured by krill (Pakhomov et al. 2002), the spreading trend could well be due to a decline in productivity in the SW Atlantic.

A decline in productivity is indicated by a comparison between surface chlorophyll concentrations recorded by the satellite-mounted Coastal Zone Colour Scanner in the seventies and eighties and the SeaWiFS satellites during the past 10 years (Gregg and Conkright 2002). The only larger-scale region of the world ocean where chlorophyll concentrations have dropped 25% over this time period is the marginal ice zone surrounding Antarctica (but not the Arctic) in spring. In contrast, the Patagonian shelf plume has increased productivity by 50% concomitantly, which could be attributed to the ongoing retreat of the Patagonian glaciers and the resultant exposure of vast stretches of glacial flour (finely ground rock) to transport by river runoff or wind-borne dust.

During the glacials, glaciers were more extensive, sea levels were lower by as much as 100 m and the continents were drier, so the extensive, exposed Patagonian shelf will have contributed much of the iron-bearing dust which fertilised the more productive glacial Southern Ocean (Abelmann et al. 2006). So why Patagonian dust is not reaching the Antarctic Circumpolar Current today is a mystery that might find its explanation in wind patterns or in differences in transport of glacial flour, as compared to dried-out, former coastal sediments. It is worth pointing out that an analogous situation to today's prevailed at the start of the Holocene, when retreating ice-age glaciers exposed large areas covered with glacial flour to the wind and rainfall, and sea level rose reducing the dust supply from the continental shelf region. Dust-borne iron supply to the ocean and accordingly productivity also declined in this period, as indicated by microfossil proxies in sediment layers laid down in the transition from the last glacial maximum to the Holocene (Abelmann et al. 2006).

The glaciers on the Antarctic Peninsula have also retreated dramatically as a result of global warming, but because of the rugged terrain and absence of flatland not much dust is likely to be mobilised from here. Nevertheless, there should be more glacial flour transported by runoff to the coastal waters of the APP. The extent to which iron from this source can be utilised and subsequently recycled and transported out into the open ocean along the APP will need to be investigated. Iron can also be supplied by water coming into contact with sediments in the course of upwelling along the

continental slope of the western Peninsula, which explains patches of higher productivity there. However, the mechanisms of iron supply to overlying water, but also replenishment of iron in the source sediments of the slope, the size of the sedimentary source and the rate of iron flux in relation to other nutrients would need to be assessed before the impact of this source can be quantified. In any case, as most of the APP overlies deep ocean, the area impacted by slope-supplied iron is relatively small. Other potential sources of iron that can fluctuate are hydrothermal vents, which need to be considered here because the APP overlies a tectonically active area. There is evidence of hydrothermal activity but currently no information on iron input. Summing up, it does not appear that a decline in productivity of the APP, if such a thing is true, can be attributed to an overall decrease in input of "new" iron to open waters.

An alternative explanation for the krill decline is more frequent recruitment failure during the past decades related to the retreating expanse of winter sea ice (Atkinson et al. 2004). Since years with more ice result in larger krill stocks, there must be a beneficial effect of sea ice on krill recruitment. However, sea ice in the Southern Ocean (in contrast to the Arctic) has only retreated in the region of the APP as a result of global warming, so this particular stretch would have to be crucial to krill recruitment (Smetacek and Nicol 2005). Since the seasonally retreating ice cover crosses the continental slope (the site of krill larval ascent) all around Antarctica, one might wonder why only some stretches are important nursery grounds. Possibly the congruence between iron supply from continental sources and sea-ice cover along the APP is the reason for the beneficial effect. Ice algal growth and subsequently that of blooms developing in iron-fertilised, melt-water stabilised layers at the marginal ice zone enabled the krill larvae to grow faster and hence recruit more biomass into the adult population. It has even been suggested, based on evidence gleaned from whaling records, that the ice edge in the APP has retreated significantly during the last century (De la Mare 1997). If sea-ice retreat is indeed the reason, then the decline in krill stocks would have happened anyway and, if whale populations had not been exploited or had since recovered, they would now be undergoing, or at least facing, severe starvation.

Investigations of krill occurrence and density under sea-ice cover indicate that distribution is highly patchy, as is also that of sea-ice algae. The greatest krill densities are found in association with sea-ice floes coloured brown with algal growth (photo 2.8). Krill are generally absent from barren, white

sea ice (personal observations). The provenance of sea ice with differing algal concentrations could be related to the time of formation. Thus, the first layer of sea ice that forms over autumn water will incorporate the largest load of suspended particles, including not only algae and bacteria but also detritus. Since the water column under sea ice is remarkably transparent, the missing particles could only have sunk out or been incorporated into the growing ice matrix. Evidence from sediment trap catches (lack of an autumn peak in flux) and investigations of "first flush" floes support the latter fate. The layer of ice crystals (frazil ice) that forms on the surface layer when cold winds blow over the ocean, and prior to compaction into floes, acts as a "sponge" that "filters" particles out of the water column. As ice forms, brine is discharged which homogenises the water column vertically and replenishes the pore water within the surface ice matrix, which eventually compacts into floes. These first-flush floes subsequently get pushed on top of each other in pressure ridges, so that new floes form in the temporary stretches of open water formed as a result. Brine discharged during the freezing of these later floes will mix the water column deeper than the previous mixed layer, bringing up particle impoverished, sub-surface water. So the later in winter the floes form, the less particles, but also iron, they contain. Since first-flush floes are mixed with younger, hence barren ones forming over clear water,

Photo 2.8: An ice floe raised by surface waves shows the ice-algae layer on its undersurface, the ideal habitat for krill

the distribution of productive and barren floes in the ice cover will be highly patchy but accessible to exploitation by the swimming abilities of krill. So the size and mobility of krill enable it to make optimum use of the patchiness inherent to the sea-ice habitat.

One of the questions discussed at the time of the *Discovery* surveys was whether krill was an animal of the pack ice or the open, ice-free ocean. Marr's (1962) detailed monograph on the biology of krill, which was widely accepted, came down strongly against any role for sea ice. He ridiculed the accounts of whaling captains of krill observed on the underside of overturned ice floes. Marr's view was based on the results of a cruise which had entered the pack ice but failed to catch any krill in vertical net hauls. We now know from direct observations by divers and cameras that the krill assemble on the ice undersurface, so cannot be caught by nets pulled through the water column. Now that the importance of ice as a winter habitat for krill seems to be widely accepted, one needs to remember that half the krill habitat in the APP is permanently open water. Satellites indicate a great deal of meso-scale patchiness, due probably to hydrographical features in the APP. However, the density of krill stocks prevalent in the APP prior to whaling is difficult to imagine today. We only know that it must have been there since so many whales were dependent on it. So is the decline of krill in the aftermath of whaling pure coincidence, and would it now be causing the starvation of the whales had they not already been depleted? In the following section, I argue that the simple "food chain of the giants" (diatoms-krill-whales) was maintained precisely by the giants. The formerly massive krill stocks declined with the whales, leaving no krill surplus behind. And now the APP seems to be reverting to the status of a "normal" stretch of salp-dominated HNLC ocean.

2.7. ECOSYSTEM CONDITIONING BY THE "FOOD CHAIN OF THE GIANTS"

So how could the top predators enhance the population size of their prey? The answer would be by disrupting the "normal" course of events, i.e., the mechanisms and pathways along which pelagic ecosystems run in the absence of large whale densities. But first of all one needs to acquire a quantitative picture of the animal densities prevalent in this area prior to whaling. This can be achieved by reading the reports written by Hardy (1967) on board the *Discovery* cruises at the height of the whaling. According to his diaries, great whales,

generally in groups, were encountered more or less daily in the Antarctic Circumpolar Current south of Africa. In striking contrast, I have seen only 10-20 minke whales in this region, but less than a handful of great whales, in the course of six two-month research cruises at different seasons over the past 15 years on board RV *Polarstern*.

One of these cruises was spent in the ice edge zone of the Scotia Sea (APP), where we saw no large whales but instead observed a krill swarm move into and graze down, in the course of several hours, a diatom bloom we were studying during a long-term station. The krill densities were so large that they interfered with light measurements and left behind ammonia concentrations never before recorded from the surface ACC (Treguer and Jacques 1992). The diatom species grazed down by the krill, a typical ice-edge flora, were replaced by cryptophytes. Although difficult to quantify, the impact of the krill swarm on the entire pelagic biota was immense. The analogy with a locust swarm or a herd of elephants arose when the data became available, shortly after the krill swarm left. Surely such a swarm must also influence the iron budget, whether by exporting it out of the system in sinking faeces or by stepping up the rate of recycling. The krill swarm mentioned above left behind plenty of faecal matter in the water column, but their patterns of vertical distribution did not suggest export as the main fate (González 1992). The impression gained was that the bulk was recycled in the surface layer.

It would be interesting to follow the fate of iron in phytoplankton communities grazed by krill. The point is that such krill swarms must have been much more plentiful in the past. Indeed, their densities would have resulted in regular "conditioning" of the environment. Thus, the krill grazing pressure we observed led to transfer of essential nutrients from the classic, ice-edge diatom bloom (dominated by small pennates) to a flagellate bloom which most likely developed because the krill had removed their protistan grazers such as ciliates together with the diatoms. The effect would enhance recycling and prolong the lifetime of individual iron atoms in the surface layer.

The krill swarm was followed by petrels, but mammals were conspicuous by their absence. Such krill swarms will have been the target of the abundant great whales prior to whaling. Since the whales were eating protein but accumulating lipids, they were sequestering energy and could well have been recycling essential elements, in particular iron, back to the ecosystem for phytoplankton to fix more energy. The faeces of marine birds and mammals tend to

be fluid (photo 2.9) and, being warm, rise to the surface before being dispersed (I have seen this happening). Taking the terrestrial analogy of savannahs and steppes, where the growth of grasses favoured by herbivorous ungulates as food is also promoted by them, I have come to speculate that whale feeding behaviour and their waste products conditioned the surface layer in a way that promoted the abundance of krill. Dung beetles and earthworms mediate between ungulate faeces and grasses in the soil, so it is possible that some zoo-plankton such as *Oithona* or the harpacticoid *Microsetella* play a similar role in the pelagial. Such a "manuring mechanism" by the giants would have increased the spatial extent of the productive region. In their absence, recycled productivity has gone down, the productive area has shrunk and salps have moved in.

An additional mechanism by which swimming animals, including zooplank-ton larger than a centimetre, can influence their environment is by turbulent mixing of the deep water column below the depth of wind mixing. This sur-prising effect, first broached on the basis of theoretical considerations by

Photo 2.9: A minke whale that had been feeding on krill, photographed in the Antarctic Penin-sula Plume while defecating in surface water. Note the fluid nature of the faeces.

Source: Smetacek and Nicol 2005. Our thanks to Captain J. Borkowski III of RV *Nathaniel Palmer* for his kind permission to reprint this photo.

Huntley and Zhou (2004) and now confirmed by field measurements of vertically migrating North Pacific krill (*Euphausia pacifica*), has the potential to enhance nutrient input through the pycnocline to the surface layer (Kunze et al. 2006). Given the high densities of krill and whales that prevailed in the APP 100 years ago, the effect must have been quite significant. It has even been suggested that the global depletion of fish and whale stocks could have a measurable impact on the intensity of the ocean's conveyor belt and hence climate, because of declining turbulent mixing in the deep ocean (Kerr 2006). The impact of this "stirring" effect needs to be investigated in different regions, but it is a good example of how large animals can modify their environment by conditioning it.

It should be noted that the beneficial effects of environmental conditioning, whether by manuring or stirring or both, increase with the increasing density of the whale population. A limit is imposed by the carrying capacity of the system, i.e., when competition for resources within the population constrains recruitment. However, in the context of environmental conditioning, carrying capacity is linked with population size in a dynamic way. It is likely that whale populations in the past glacials were larger and their connections to diatoms and krill tighter, because the seasonal sea-ice zone was more extensive and also more productive due to enhanced dust input (Abelmann et al. 2006). Further, the total area of the habitat will have been larger, due to equatorward displacement of the sea ice edge. It is possible that the absence in the ACC of planktivorous swarm-building small fish like sardines is due to the past predation pressure of baleen whales. The low temperatures apparently render fish more vulnerable to attack by warm-blooded predators, unlike invertebrates such as cephalopods and krill that seem to retain their agility over a broader temperature range.

The question arising in this connection is: which type or stage of pelagic system would sequester more CO_2 per iron atom from the atmosphere? The boom-and-bust system of a diatom bloom which exports large amounts of new biomass including iron to depth early in the growth season (Smetacek et al. 2004), or the recycling system where the bloom is grazed down and prevented from sinking out? The waste products of recycling would subsequently be returned to a system altered by the feeding activity of the herbivores. The latter system would also suffer losses to sinking particles albeit over a longer period, during which energy in the form of lipids, channelled off the spinning wheel of iron-based regenerated production, could accumulate in herbivores and predators over annual cycles.

It should be pointed out that copepod stock sizes in the ACC may be in the same range as the biomasses of phytoplankton blooms (Henjes et al. 2007). Such a large zooplankton population would need to eat three times the biomass in the surrounding water to double its own, assuming a 30% ecological efficiency. So the grazing impact, even just of copepods, is large and could have been even larger when the krill were still around (figure 2.4). So the above question boils down to: does the Fe:C ratio of sinking particles rise or fall along the gradient from fresh diatom cells to reworked faeces? Indeed, does iron sink out as insoluble rust particles in the course of regenerated production or is it always bound to some organic molecule whether in dissolved or particulate form? The fertilisation experiments indicate otherwise, because the colloidal ferric hydroxide precipitate that must have formed as the acidified ferrous sulphate solution released from the ship mixed with alkaline sea water, was more or less quantitatively utilised by

Figure 2.4: Accumulation of broken and empty diatom siliceous shells (frustules per litre) as an indicator of copepod grazing within and outside an iron-fertilised patch, recorded during the EisenEx experiment
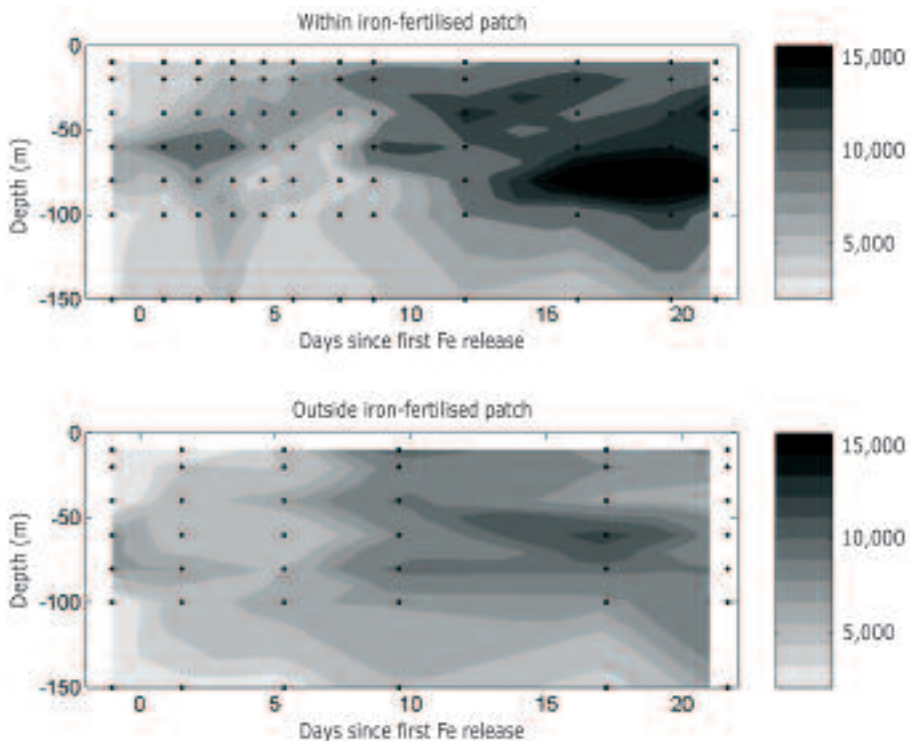
Source: Assmy et al. 2004. Data from P. Assmy, AWI.

diatoms. So, little iron was lost, although this form of input is definitely the most likely to result in sinking out before utilisation: precisely the fate predicted before the first experiments. Either diatoms can take up insoluble ferric hydroxide or it is made accessible in another form by some mechanisms involving ligands (iron-binding organic molecules) present in the water.

2.8. TESTING THE HYPOTHESIS

The hypothetical relationships dealt with above cannot be observed in field investigations carried out along transects and grids, and nor can they be studied in enclosure experiments. In situ iron fertilisation experiments have emerged in the last 10 years as a reliable method for testing biogeochemical and ecological hypotheses not accessible by other means. Larger-scale experiments than those above, carried out in the APP itself, would enable us to determine the current extent of food limitation of krill. Thus if an extensive bloom was induced by fertilisation, and a krill swarm present in the area responded to it by increasing grazing rates, individual weights and egg production rates, a case would be made for food limitation. Such a response was recently demonstrated for a copepod species (*Rhincalanus gigas*), which developed its gonads and laid unusually high numbers of eggs after stimulation by an iron-fertilised bloom (Jansen et al. 2006). The impact on salps could be derived as well: if their numbers declined in the bloom, then they would indeed be creatures of low-productive waters. If they grew in the bloom, then they would be competitors of the krill as some suggest. In either case, we would advance our knowledge and understanding of pelagic food webs.

An iron-fertilisation experiment carried out in the APP to extend the growth season by supplementing the iron supply to the regenerating, summer system would not only test the recycling hypothesis, with its prospects for boosting today's declining krill stocks, but also the iron hypothesis of John Martin (1990), with its CO_2 sequestering intention. Both hypotheses address fundamental questions of integrated Earth system science that are relevant to our understanding of the role of the marine biosphere in past and ongoing climate change. They would not only provide basic information on the structure and functioning of pelagic ecosystems, but would also help validate various proxies for palaeoproductivity and glacial CO_2 drawdown. Measuring the composition and magnitude of vertical flux (ungrazed phyto-

plankton vs. zooplankton faeces) would help us learn how to optimise the fertilisation technique so as to sequester as much carbon per unit iron as possible. It should be pointed out that if all the unused macronutrients in the HNLC ACC were taken up by phytoplankton and converted to biomass in the 60 m mixed surface layer, the amount of carbon dioxide drawn down from the atmosphere to compensate the resultant deficit would be approximately equivalent to the annual rate of accumulation of anthropogenic CO_2 in the atmosphere (approximately 3 gigatonnes). The frequency with which this amount could be taken up is not clear, but it is too much for humankind not to consider this option seriously. If krill and whales can profit from this fertilisation, so much the better. It would be the marine equivalent of ecosystem restoration and maintenance.

2.9. CONCLUSIONS

As pointed out above, the real paradox of the Antarctic seasonal sea-ice zone is, or rather, was, the concentration of large animal stocks, specifically krill and its air-breathing vertebrate predators, in a relatively small region, the Antarctic Peninsula Plume, characterised today by moderate productivity. Unfortunately, the "food chain of the giants" no longer exists, so it cannot be investigated and its structure and primary productivity patterns compared with regions like the Ross Sea to ascertain the mechanisms maintaining high animal biomass concentrations. The "rule of thumb" ecological transfer efficiencies of 10:1 between trophic levels very evidently did not apply here, implying that this "food chain of the giants" must have functioned differently, channelling energy to higher trophic levels with greater efficiency than food chains quantified elsewhere. However, as shown by Jackson et al. (2001) in an assessment of lower latitude coastal ecosystems, stocks of large marine animals prior to human exploitation must have been much larger than they have been since historical times. So perhaps the Antarctic paradox is merely due to the fact that, because of its inaccessibility, this ocean was the last marine ecosystem to be fully exploited by humans and in a period when the decimation could be documented systematically (Smetacek and Nicol 2005).

The reconstructed krill densities of the first third of the twentieth century are hard to believe in comparison to today. Clearly, krill stocks must have declined significantly. The sea-ice retreat along the Peninsula, due to global warming, is believed to have affected krill recruitment, because the sea ice in

this region provides protection and food in the form of ice algae to ascending krill larvae. I have argued that the ongoing decline of krill stocks is a result of the collapse of the diatom-krill-whale food chain following the removal of the whales. Although the effect of sea-ice retreat due to global warming cannot be ignored as a cause of krill decline, the role of whales in maintaining high phytoplankton productivity and hence high krill biomass by virtue of iron recycling is likely to have been more significant. I base this conclusion on the following considerations:

1. The decline in whale stocks was not accompanied by a significant increase in the stock sizes of other smaller krill predators, implying that a krill surplus did not accumulate after the whales were removed.

2. The productivity of the area occupied by the "food chain of the giants" has apparently gone down, as indicated by a comparison with satellite images made in the 1970s (CZCS) with those of the 2000s (SeaWiFS).

3. The spread of salps in the same region is also an indicator of declining productivity.

4. The decline in productivity is unlikely to be due to a decline in input of "new" iron, but is more likely the result of a decline in recycled iron released by the feeding of the whales and krill.

The "iron recycling hypothesis" to explain declining krill stocks can be tested via a large-scale iron fertilisation experiment in the Scotia Sea. Apart from furthering our understanding of pelagic ecosystem functioning, an added benefit of such experiments would be to test the feasibility of larger-scale iron fertilisation to sequester significant quantities of atmospheric CO_2 and hence mitigate the effects of climate change, not only on polar but also global ecosystems. Antarctic sea ice is not threatened by a rapid retreat in the course of this century, as is happening with the Arctic ice pack. However, if atmospheric CO_2 concentrations are allowed to rise over the next century, there can be little doubt that the southern sea ice and its ice-dependent ecosystem will also be seriously affected.

ACKNOWLEDGEMENTS

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