EXPLOITATION OF THE MARINE ECOSYSTEM IN THE SUB-ANTARCTIC: HISTORICAL IMPACTS AND CURRENT CONSEQUENCES

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(with one text-figure)

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The Southern Ocean is often portrayed as the last great wilderness. However, the marine living resources of the sub-Antarctic islands have been harvested for over two centuries. Exploitation began with the upper trophic levels and the high-value air-breathing species, before progressing down the food chain to the lower trophic levels and the less valuable nekton and zooplankton. Exploitation in the sub-Antarctic began in the late eighteenth century, nowhere better typified than at South Georgia. At South Georgia exploitation started with Antarctic Fur Seals, *Arctocephalus gazella*, which were reduced almost to extinction by the mid-nineteenth century. As the fur trade rapidly became uneconomic, new targets were sought and by the end of the nineteenth century, oilers were hunting for Southern Elephant Seals, *Mirounga leonina*, Southern Right Whales, *Eubalaena australis*, and some sub-Antarctic penguin species. As these stocks also declined and their com-mercial exploitation became uneconomic, the focus shifted such that by the beginning of the twentieth century, harvesting for other baleen whales (the so-called rorquals) and Sperm Whales, *Physeter macrocephalus*, was well-established. With the demise of the great whales, other less valuable species were then sought, so that by the latter half of the twentieth century, fishing for finfish and krill had begun. Removal of the upper trophic level species has impacted upon the sub-Antarctic marine system resulting in profound changes, the consequences of which continue to the present. The consequences of such harvesting are reviewed in the context of an ecosystem model that demonstrates some of the expected changes in the marine foodweb that may arise as a consequence of harvesting and how, once harvesting ceases, populations may recover to their pre-exploitation state. The current status of the South Georgia foodweb is reviewed in the context of these predicted changes. In the period since uncontrolled harvesting ceased, the role of physical environmental forcing factors has been recognised and found to be key to any understanding of marine foodweb dynamics. These two major forces, historical exploitation and climate change, may act in concert to alter ecosystem dynamics. Disentangling these confounding drivers may be difficult and complex, but because of the relatively well-documented history of exploitation the sub-Antarctic may offer one location where it is feasible.

Key Words: Exploitation, marine living resources, sub-Antarctic, ecosystem effects, climate change.

THE HISTORY OF EXPLOITATION IN THE SOUTHERN OCEAN

Despite the remoteness, inhospitability and size of the Southern Ocean, the living resources of its marine ecosystems have been harvested for over two centuries. Though its remoteness from human habitation and commercial markets meant that harvesting did not begin until the late eighteeth century, the subsequent pattern of exploitation followed that of many other parts of the World Ocean. Harvesting started with the large, high-value species in the upper trophic levels, before progressing down the food chain to the smaller, less valuable species at the lower trophic levels (Pauly *et al.* 1998, Jackson *et al.* 2001).

The history of exploitation in the sub-Antarctic is exemplified by South Georgia, the crucible of exploitation for seals and the great whales in the southern hemisphere, and arguably for the world. The first recorded landing was on 17 January 1775 by the then Commander, later Captain, James Cook. The exploitation of the wildlife at South Georgia began shortly after Cook returned to Britain and reported the large numbers of fur seals found there. Sealers were initially very successful and the high rate of harvesting of Antarctic Fur Seals, *Arctocephalus gazella* (Peters, 1875), meant that the fur trade rapidly became uneconomic and new targets were sought. By the end of the nineteenth century, Southern Elephant Seals, *Mirounga leonina* (Linnaeus, 1758), Southern Right Whales, *Eubalaena australis* (Desmoulins, 1822), and some sub-Antarctic penguins were being harvested for oil. As these stocks also declined and became uneconomic, the focus shifted once again, such that by the beginning of the twentieth century, harvesting for other baleen whales and Sperm Whales, *Physeter macrocephalus* Linnaeus, 1758, was well established. With the demise of the great whales, other less valuable species were then sought, so that by the latter half of the twentieth century, fishing for finfish and Antarctic Krill, *Euphausia superba* Dana, 1852, had begun.

Much of the history of the exploitation of the Southern Ocean is well documented in previous work (Laws 1953, Bonner 1980, 1984, Everson 1977, Headland 1992, Kock 1992). The following review has drawn heavily on their source material.

The main targets for exploitation both at South Georgia and more generally in the Southern Ocean are discussed below.

Antarctic and sub-Antarctic Fur Seals

Hunting for seals began on the sub-Antarctic islands in about 1778, when Antarctic and sub-Antarctic, *Arctocephalus tropicalis* (J.E. Gray, 1872), Fur Seals were targeted for their skins (Roberts 1958, Bonner 1984). Hunting involved the taking of all demographic classes, with sealing reaching a peak in the 1800–01 season, when the 17 vessels operating at South Georgia took more than 112 000 seal skins in that season (Headland 1992). By 1822, Weddell (1825) estimated that 1 200 000 skins had been taken from South Georgia and the Antarctic Fur Seal was almost extinct on the island. This same pattern of unregulated exploitation occurred at many of the other sub-Antarctic island archipelagos, such as at Tierra del Fuego, Gough Island, Tristan da Cunha, Bouvetøya, the Prince Edward Islands, Îles de Crozet, Île de Kerguelen, McDonald Island and at Macquarie Island, albeit with different timings. Exploitation also moved further south, for example fur seals at the South Shetland Islands were first exploited in 1819–20, but the smaller stocks there and at the South Orkney Islands and the South Sandwich Islands meant these were also rapidly depleted.

Most populations of Antarctic and sub-Antarctic Fur Seals were on the verge of extinction by 1825. In subsequent years, sealing was intermittently resumed when fur seal populations showed some signs of recovery, indeed it continued until the early days of the twentieth century (Headland 1992). The last sealing expedition was to South Georgia in 1907, when 170 skins were taken (Larsen 1920).

Southern Elephant Seal

The rendering and extraction of oil from Southern Elephant Seals began towards the end of the eighteenth century when the exploitation of fur seals declined, though both species were often exploited at the same time and in parallel (Headland 1992). Oil from Southern Elephant Seals was less valuable than the skins from fur seals, it was also more labour intensive to collect; therefore Southern Elephant Seals were not pursued to the same extent as fur seals and populations were not taken to such low numbers (Bonner 1984). The large breeding colonies at South Georgia, the Île de Kerguelen, Heard Island, McDonald Island and Macquarie Island were the main centres for the sealers. Unregulated sealing stopped at most places within the first two decades of the twentieth century (Headland 1992). A controlled harvest of male Southern Elephant Seals was continued at South Georgia from 1909–1964 and at Île de Kerguelen from 1958–1961 (Bonner 1984). The harvest at South Georgia has been highlighted in the past as a good example of the rational management of a natural living resource (Laws 1953, Bonner 1958, 1984).

Seabirds

King Penguins, *Aptenodytes patagonicus* J.F. Miller, 1778, and crested penguins (*Eudyptes* spp.) were exploited for oil, food and as fuel for fire on some of the sub-Antarctic islands, such as at South Georgia, Heard Island and Macquarie Island, during the sealing period of the eighteenth and nineteenth centuries. Subsequently, the numbers of King Penguins have increased rapidly at all breeding sites – in the range of 8–12% per annum on most sub-Antarctic islands since the 1960s. The largest populations are at the Îles de Crozet (700 000 pairs), South Georgia (450 000 pairs) and Macquarie Island (110 000 pairs).

Eggs of a number of other species, including Chinstrap Penguins, *Pygoscelis antarctica* (J.R. Forster, 1781), and Adélie Penguins, *P. adeliae* (Hombron & Jacquinot, 1841), in the Antarctic and of Wandering Albatross, *Diomedea exulans* Linnaeus, 1758, and Black-browed Albatross, *Thallasarche melanophrys* (Temminck, 1828), in the sub-Antarctic were harvested by sealers and whalers well into the 1950s, when the taking of eggs ended (Bonner 1984). The effects this egging may have had on bird populations are unknown (Bonner 1984).

Whales

Commercial whaling in the Antarctic began in December 1904 at Grytviken on South Georgia. It then expanded to other locations on South Georgia and then to the more southerly islands of the Scotia Arc and to Île de Kerguelen (Bonner 1980). Until the early 1920s, whaling was essentially land-based, with catchers towing dead whales to the processing plants either at shore stations or on factory vessels moored in sheltered fjords and bays (Headland 1992). Whaling became pelagic from 1925 onwards, when factory vessels began to be fitted with stern slipways; after this, pelagic operations based around mother ships and associated catcher vessels, became the most common type of whaling.

Seven species (including subspecies) of baleen whales (Mysticeti) occur in the Southern Ocean, south of the Antarctic Polar Front, and all have been extensively exploited in the past. Of the toothed whales (Odontoceti), only Sperm Whales were taken regularly and in appreciable numbers. Killer Whales, *Orcinus orca* Linnaeus, 1758, and Southern Bottlenose Whales, *Hyperoodon planifrons* Flower, 1882, were also taken occasionally, but then only in small numbers.

Production at South Georgia, in terms of barrels of oil, peaked in the 1926–27 season, and in terms of whale numbers, the previous season (Headland 1992). More generally, across the Southern Ocean, whale catches peaked in the 1930s when pelagic operations prevailed (Bonner 1980). From this time onwards species successively became commercially unviable, and consequently smaller, less valuable species were targeted and began to form a larger proportion of the catch (Bonner 1980). The smallest species, Minke Whales, *Balaenoptera acutorostrata* Lacépède, 1804, were not exploited in appreciable numbers until the early 1970s, but they then became the main target until 1987 when major whaling operations ceased (Bonner 1980). Thus, Bonner (1984) shows that first Blue Whale, *B. musculus* (Linnaeus, 1758), then Fin Whale, *B. physalus* (Linnaeus, 1758), and eventually Sei Whale, *B. borealis* Lesson, 1828, numbers were reduced, until finally Minke Whales were targeted until the cessation of large-scale harvesting.

The total catch of whales reported from the Antarctic between 1904 and 1987 was more than 1.15 million animals or approximately 65 million tonnes (based on catch statistics held by the International Whaling Commission and assuming average weights for each species), though catch records have been revised by the IWC and will probably continue to form an area of contested discussion. A portion of this catch, in particular of Sperm Whales, Pygmy Blue Whales, *B. musculus brevicauda* Ichihara, 1966, and Sei Whales, was taken north of the Antarctic Polar Front in the 1960s and 1970s. However, it seems reasonable to assume that, prior to Antarctic whaling, nearly a million whales may have moved through the sub-Antarctic in the austral summer and autumn every year (Laws 1977). With the exception of Minke Whales, and probably Killer and Southern Bottlenose whales, the numbers of all species declined dramatically during the harvest and are currently only small fractions of their pre-exploited population sizes.

Finfish

Plans to develop fisheries for finfish in the Southern Ocean date back to the early days of land-based whaling at South Georgia in 1906 (Headland 1992), although large-scale harvesting of finfish did not begin until the late 1960s at South Georgia and the early 1970s around Île de Kerguelen (Everson 1977). After 1978, the finfish fisheries expanded to the South Orkney Islands and to more southerly grounds. These southern grounds yielded good catches for only a few years and declined rapidly by the early 1980s. Until the mid-1980s the finfish fisheries were entirely trawl fisheries.

The species that have been targeted by the trawl fisheries include Marbled Rockcod, *Notothenia rossii* Richardson, 1844; Mackerel Icefish, *Champsocephalus gunnari* Lönnberg, 1905; Grey Rockcod, *Lepidonotothen squamifrons* (Günther, 1880); Yellowfin Notothen, *Patagonotothen guntheri* (Norman, 1937); Sub-Antarctic Lanternfish, most plausibly *Electrona carlsberg* (Tånning, 1932); and Wilson's Icefish, *Chaenodraco wilsoni* Regan, 1914, (Kock 1992). Frequent by-catch species have included various icefish species, Humped Rockcod, *Gobionotothen gibberifrons* (Lönnberg, 1905) and skates, (*Amblyraja georgiana* (Norman, 1938) and *Bathyraja* spp.) (Kock 1992). Most species have been harvested for human food, while the lanternfish, and in some cases, the retained by-catch species, were mainly used for fishmeal (Kock 1992).

Catches for some targeted species were initially high, but declined very rapidly thereafter. For example, Marbled Rockcod catches at South Georgia were initially very high, with approximately 400 000 tonnes in the first season in 1969–1970 and approximately 100 000 tonnes the following season. The stock was so depleted by this initial take, that biomass has remained low ever since and has not recovered some 40 years later (Kock 1992). The same patterns were seen elsewhere in the Antarctic, principally at the South Orkney Islands, the Antarctic Peninsula and Île de Kerguelen (Kock 1992).

In the mid-1980s demersal longlines were introduced to catch Patagonian Toothfish, *Dissostichus eleginoides* Smitt, 1898, primarily around South Georgia and at the Île de Kerguelen as well around other sub-Antarctic islands (Agnew 2004).

Antarctic Krill

Fishing for Antarctic Krill began on a commercial scale in 1972 (www.fao.org; accessed 26 June 2009), starting at South Georgia in 1975–76 (Agnew 2004). It rapidly focused on three main fishing grounds: to the east of South Georgia, around the South Orkney Islands and to the north of the South Shetland Islands. Catches peaked in 1981–82, when 528 201 tonnes were landed, 93% of which was taken by the Soviet Union. In the following years catches stabilised at approximately 300 000–400 000 tonnes, or about 13% of the world catch of crustaceans at that time (www.fao.org). When economic factors forced the Soviet fleet to stop fishing, catches declined dramatically after 1991–92 to about 100 000 tonnes per annum.

ECOSYSTEM CONSEQUENCES OF EXPLOITATION OF THE SUB-ANTARCTIC

The ecosystem consequences of such a large and rapid removal of upper-trophic level species have been the subject of a great deal of scientific debate, conjecture and disagreement (see for example Ainley *et al.* 2007 and Nicol *et al.* 2007 and references therein). Of course the difficulty in determining and quantifying what effects might have been propagated through the Antarctic and sub-Antarctic ecosystem is that there is no information upon which to assess the pre-exploitation status of the marine system. While it is possible to make some qualitative inferences that fur seals were very numerous, prompting Cook to return home with the descriptions that enticed sealers to venture to these new areas, quantitative assessment is not now possible. Nevertheless, it is feasible to examine potential scenarios using mathematical models that provide a representation of the operation of the Antarctic and sub-Antarctic marine ecosystem (see Hill *et al.* 2006 for review). In this paper, rather than consider the merits of different models, we use the model of Murphy (1995) as an illustration of the potential changes in linked predator and prey species that might have arisen from historical exploitation and the subsequent trajectories that populations follow upon the cessation of harvesting. This model is based upon the "krill-centric" ecosystem of the South Georgia region and describes the population trajectories of seals, penguins, whales and krill from the period prior to the discovery of South Georgia to beyond the present day (fig. 1).

In the context of the Murphy (1995) model (hereafter simply referred to as "the model") the present day is approximately the year 2000. Here we compare contemporary data on the trends in the population size of the key ecosystem components (seals, penguins, whales and krill), with their population trajectories described by the model.

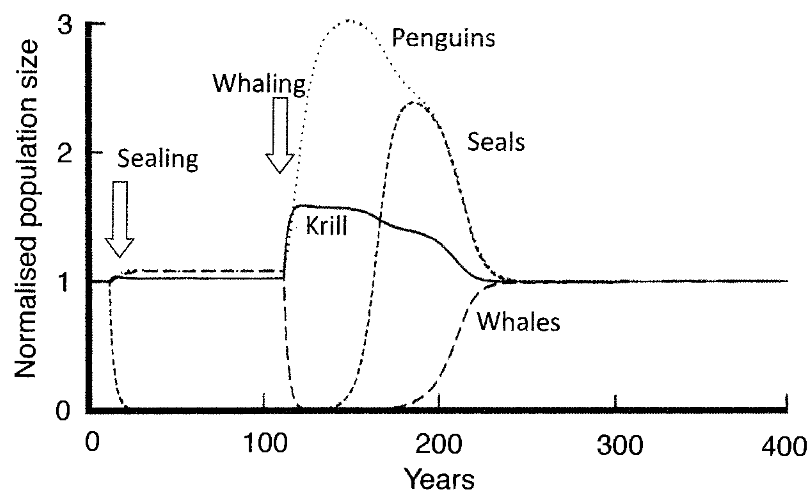

FIG. 1 — Output of a simulation model to examine the impacts of harvesting (sealing and whaling), on other ecosystem components; modified from Murphy (1995) with permission of the author.

Fur seals

The model indicates that population of fur seals would currently be in a period where the growth rate has slowed, or even stopped, following a period of rapid increase. Recent data on the population size of fur seals is lacking. However, the most recent survey of the South Georgia population, carried out in 1991 (Boyd 1993), indicated that the population growth rate had decreased from the exceptionally high 16.8% in the period 1955–71 (Payne 1977) to 9.8% in the period 1977–90. Data from long-term monitoring at a seal study areas on Bird Island (see Forcada *et al.* 2005) indicate that the number of pups born annually on that beach has also actually decreased over the period 1984–85 to 2003–04.

Penguins

The model indicates that penguin populations would now be in decline, following a rapid increase associated with the removal of potentially competing species that consumed the same prey. The major krill-consuming penguin species at South Georgia is the Macaroni Penguin, *Eudyptes chrysolophus* (Brandt, 1837), (Croxall & Prince 1980) and data from Bird Island indicate that the population there has fallen by almost 50% over the past two decades between 1980 and 2000 (Trathan *et al.* 1998, Trathan 2004).

Whales

The increase in the number of whales indicated by the model is difficult to compare with any contemporary data because of the paucity of whale population survey data from the South Georgia region (or indeed from any other part of the sub-Antarctic). However, it is possible to infer the likely changes in numbers of whales in the region based on knowledge of the changes in breeding population size, from counts in the calving areas, of whale stocks that forage in the South Georgia region. Two such stocks, both of which feed around South Georgia during the summer months and both of which are increasing, are the Humpback Whales and Southern Right Whales that calve in the coastal waters off Brazil and Argentina respectively (Zerbini *et al.* 2004; Leaper *et al.* 2006).

Krill

The model clearly indicates that there is an expectation of a declining krill population and data from a variety of net samples collected over the period 1976–2003 indicate that there has actually been a decline in krill in the southwest Atlantic region, possibly of >50% (Atkinson *et al.* 2004, 2008).

From the summary above it is now apparent that there are indications of change in the populations of the taxa represented in the model and that these are broadly consistent with the predictions of the model. There is, of course, a number of caveats, as with any model that attempts to represent a subset of the real world. We do not raise these as a criticism of the model, simply as a reflection of the difficulty in parameterising both the individual components and the covariation between them given the uncertainties in those factors.

Such uncertainties can arise from inadequacies in the available data, for example the model "assumes" that there was a cessation in the commercial exploitation of the great whales following the moratorium introduced in 1987. However, it is now clear that illegal whaling occurred in areas of the Southern Ocean subsequent to the introduction of that moratorium (see for example, Clapham & Yushenko 2009). This has the potential to delay the recovery of whale populations as well as to influence other components of the model that are linked to the consumption of krill by those whales.

Uncertainties also arise from some (possibly) small-scale interactions that were not included in the model. Thus, in the model, penguin population processes might be perceived as responding to changes in prey abundance introduced into the model by population of other species, particularly marine mammals. However, as described above, populations of some penguin species were also heavily exploited and their population processes might equally be responding to this historical harvest. Thus, though it is important to recognise that the harvesting of penguins is unlikely to have had the same scale of ecosystem consequences as those that involved marine mammals (given their lower biomass prior to commercial exploitation), it is likely to have had at least some impact upon some population trajectories over the same time-scales.

Uncertainties also arise from effects not perceived as important at the time the model was developed, but which have subsequently been shown to be of major importance. Thus, one of the critical assumptions of the model described here is that it seeks to describe causes and effects. Thus, when an ecological force (in this case the exploitation of seals and whales) is applied, the ecosystem responds, and when the force is removed (that is, sealing and whaling cease) the system returns to its initial pre-exploitation state following some time period that accounts for ecosystem lags and interactions. However, it is now apparent from long-term studies of populations of seals, penguins and whales (Forcada *et al.* 2005, Trathan *et al.* 2006, Leaper *et al.* 2006), that climate variability can impact the reproductive output and population trajectory of these species, mediated through their prey, Antarctic Krill (Murphy *et al.* 2007). Indeed, Whitehouse *et al.* (2008) have recently shown that over the period 1925–2006, there have been long-term changes in ocean temperatures at South Georgia at a scale that would be expected to impact upon Antarctic Krill and hence the reproductive performance of seals, penguins and whales. However, it not currently possible to estimate the species-specific consequence of such changes, given the differences in the magnitude and the time lag of response for each taxonomic group. Nevertheless, it is important to recognise that the interacting forces of historical exploitation and changes in ecosystem operation brought about by changes in regional climate will have a strong influence on the population trajectories of species and their return to any pre-exploitation state.

This confounding interaction between the consequences of historical exploitation and changing climate makes the interpretation of present-day signals of climate change problematic (Croxall *et al.* 2002). For example, in describing the decline in krill, Atkinson *et al.* (2004) provided a plausible link between the decline in the spatial extent and duration of sea-ice and declining krill populations over the same time-period (since sea-ice provides a critical habitat for the early life-history stages of krill). However, such a decline in krill should be anticipated anyway, simply as a consequence of the population processes associated with the historical exploitation of krill predators. In this case the two drivers of change, historical exploitation and recent sea-ice reduction, would have a complementary effect on the population of krill such that climate-related changes could accelerate a decrease that was already occurring as a legacy of historical exploitation.

Such confounding interactions are not unique to the sub-Antarctic; the World Ocean has been highly perturbed by exploitation (see Myers & Worm 2003, 2005) and is now responding in different ways to changes in climate. However, one aspect that potentially makes the sub-Antarctic different to other parts of the World Ocean is the rates of these changes. While humans had been removing large, air-breathing species such as whales and seals from more accessible regions of the Atlantic and Pacific for several centuries, the changes in the Southern Ocean have only occurred over a 200-year time span. During this relatively recent time period, the level of exploitation has been unusually well-documented; at least in comparison with other areas of the World Ocean. Similarly, while there has been a great deal of variability in the response of the World Ocean to climate change, it is the southwest Atlantic sector, including the Antarctic Peninsula, that is warming more rapidly than almost any region on the planet (Vaughan *et al.* 2003, Turner & Overland 2009). Therefore, while it may be easy to point to the interacting forces and the consequent difficulties of distinguishing the combined drivers of change, it may be that the sub-Antarctic actually provides a unique region within which to consider the interacting historical and contemporary drivers of change.

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