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## FORUM

### THE ROSS SEA, ANTARCTICA, WHERE ALL ECOSYSTEM PROCESSES STILL REMAIN FOR STUDY, BUT MAYBE NOT FOR LONG

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#### SUMMARY

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The Ross Sea is a well-defined embayment of Antarctica about the size of southern Europe, bounded by Victoria Land to the west, King Edward VII Peninsula, Marie Byrd Land to the east, the Ross Ice Shelf to the south, and the Pacific Sector of the Southern Ocean to the north. Its waters are composed of two related biotic systems: the Ross Sea Shelf Ecosystem (RSShelfE) and the Ross Sea Slope Ecosystem (RSSlopeE). The Ross Sea is off limits to mineral extraction, but pressures on its biological resources are growing. The economic value of the resources should be weighed against the value of the system as a unique scientific resource. The Ross Sea represents an unparalleled natural laboratory in which the results of different fishery management strategies could be modeled in the context of short-term and decadal variation in biological populations, with these models applied throughout the Southern Ocean and elsewhere. The RSShelfE is the last Large Marine Ecosystem on Earth (except the Weddell Sea and, perhaps, Hudson Bay in the north of Canada) that has escaped direct anthropogenic alteration; the RSSlopeE, similar to all of Earth's other marine ecosystems, has lost its large baleen whales but otherwise is intact. A huge multidisciplinary, international scientific effort has been invested in studies of the geology, physics and biology of the Ross Sea over the past 45 years. In particular the activities of the United States, New Zealand and Italian Antarctic programmes have been models of international scientific cooperation and collaboration. The successful result is an incredible wealth of knowledge, including long-term biological data sets, not available anywhere else in the Antarctic, which have documented clear signals of climate forcing, as well as top-down influences not confused by human exploitation or activity. Ironically, much remains unknown about how these ecosystems function.

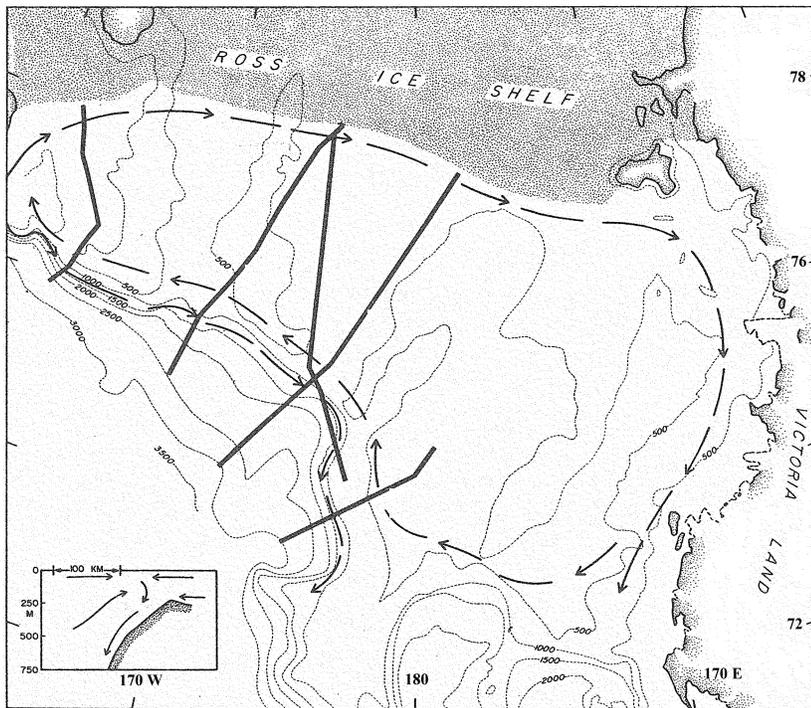
Key words: Ross Sea, Antarctica, Large Marine Ecosystem, conservation

#### BACKGROUND

The area of interest lies south of and shallower than the 3000-m isobath, which is the dividing line between the lower continental slope and the deep ocean. This boundary extends from 69°S, 170°E (off Cape Adare, Victoria Land) to 76°S, 155°W (off King Edward VII Peninsula, Marie Byrd Land). Included is a northward bend of the isobath, around Iselin Bank, to about 69°S, 175°W. This region, which is about 598 000 km<sup>2</sup>, includes the continental slope (500–3000 m) and the continental shelf of the Ross Sea (Fig. 1). Ichii *et al.* (1998) also included both the slope and the

shelf to define the 'Ross Sea'. Except for coastal polynyas, the Ross Sea is completely covered by sea ice from about April through October; its eastern portion remains covered throughout the year.

The Ross Sea Shelf Ecosystem (RSShelfE) is one of the few remaining Large Marine Ecosystems (LME; *sensu* Sherman *et al.* 1990, 1993) where human influences have been minimal. Therefore, neither top-down nor bottom-up forcing mechanisms have been compromised. The RSShelfE may be the last LME on Earth (except perhaps the Weddell Sea elsewhere in Antarctica and



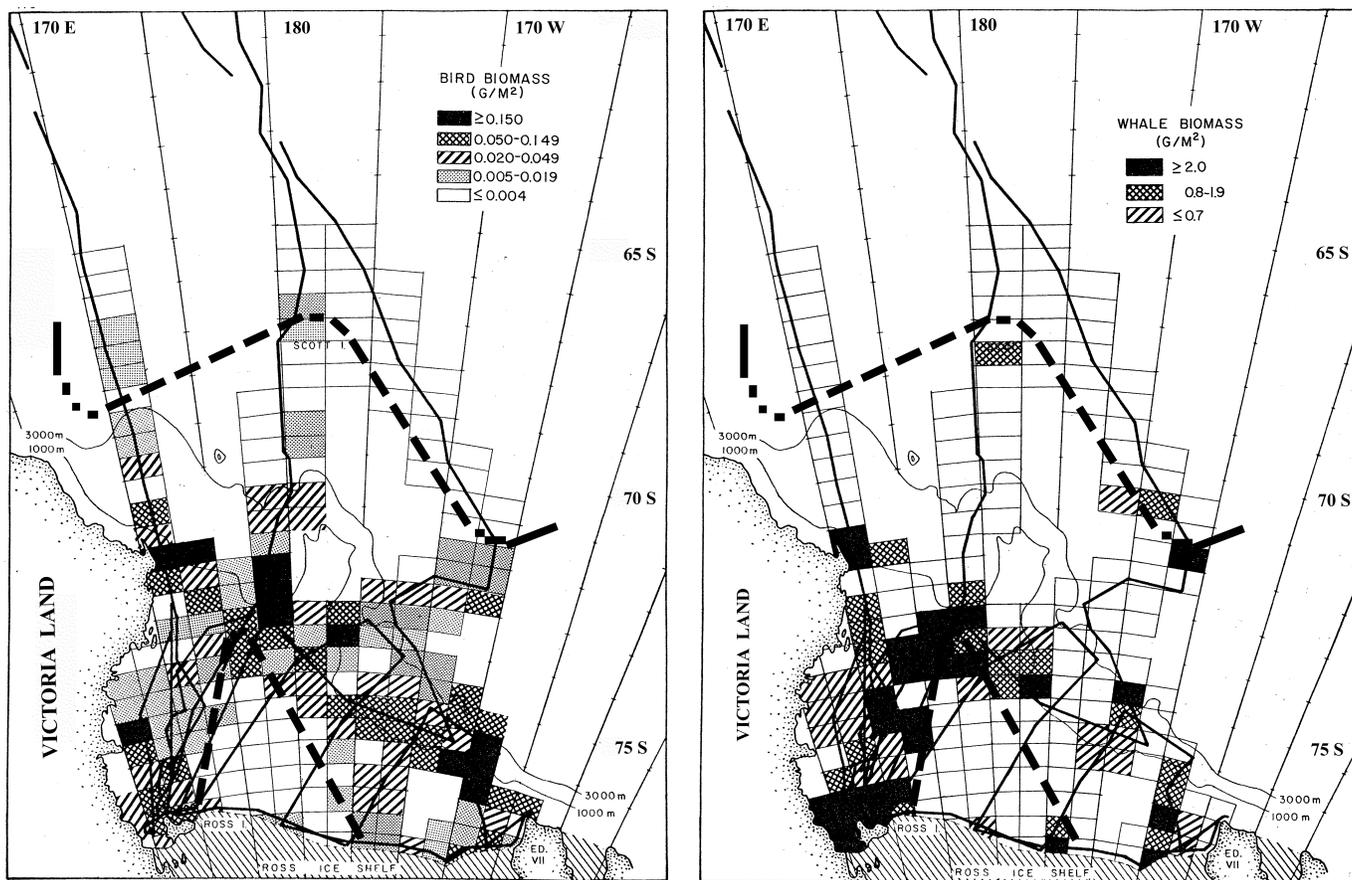
**Fig. 1.** The Ross Sea showing horizontal and vertical (insert) circulation at the surface. Transect lines are referred to in Ainley & Jacobs (1981) from which this figure was redrawn, and show where the vertical circulation was investigated.

Hudson Bay in the north of Canada; A.J. Gaston, pers. comm.) where this is the case. Other than a recent, and at present small-scale, experimental fishery for Antarctic Toothfish *Dissostichus mawsoni* on the shelf (589 tonnes in 2000; Smith 2001, Waterhouse 2001) and, for the past 14 years, a scientific take of Antarctic Minke Whales *Balaenoptera bonaerensis* mostly along the continental slope (Ross Sea Slope Ecosystem, 80 whales/year; Ichii *et al.* 1998, Brown & Brownell 2001), there has been no direct human influence. There have been no oil spills or other significant pollution, no gill netting nor trawling with associated 'by-catch', and no over-exploitation of forage- or upper-level fish by industrial fisheries. Moreover, no top-trophic predator populations have been reduced by the introduction of feral animals. Finally, to no appreciable degree had the great whales nor various commercially exploited pinniped species ever frequented RSShelfE waters and, therefore, their demise in all the other oceans and seas of the world has been neutral to this particular LME.

On the other hand, the RSShelfE has not been ignored scientifically. Its marine geology is as well known as most other continental shelves. This is the result of decades of research during which myriads of sediment cores and seismic profiles have been obtained. In part this effort has been stimulated by interest in climate change and the history of the West Antarctic Ice Sheet, which during the last glacial maximum had overlain the entire Ross Embayment (now only half; e.g. Stuiver *et al.* 1981, Anderson 2000). The basic RSShelfE physical oceanography also has been well investigated, beginning in the 1960s through R.V. *Eltanin* surveys and later projects such as RISP (Ross Ice Shelf Project), WOCE (World Ocean Circulation Experiment) and JGOFS (Joint Geophysical Ocean Flux Study). Included has been ample work on small-scale current patterns and sea-ice dynamics (e.g. Barry 1988, Jacobs & Comiso 1989, Jacobs & Giulivi 1998, Jacobs *et al.* 2002, Diniman *et al.* in press). Biogeophysical processes that contribute to sediment histories have also been well researched (e.g. such projects as ROAVERRS; Research on Ocean

and Atmospheric Variability and Ecosystem Response in the Ross Sea). Much has been learned about primary productivity (studies by S. El Sayed, O. Holm-Hanson, W. Smith and ROAVERRS over three decades; e.g. Smith & Sakshaug 1990), and the ecology of its fast ice epontic microalgae and microbial communities is better known than anywhere in the Antarctic (studies by C. Sullivan and colleagues, e.g. Ackley & Sullivan 1994, Arrigo *et al.* 1994, Fritsen *et al.* 1994, Garrison *et al.* 1986, Grossi *et al.* 1987). Organisms in the top-trophic levels are well known: its baleen whales (Ainley 1985, Ichii *et al.* 1998, Branch & Butterworth 2001), seals (Testa & Siniff 1987, Testa *et al.* 1990, and the Antarctic Pack Ice Seals project, APIS), and birds (e.g. Ainley *et al.* 1983, 1984, 1998). The presence of a distinct, fish-eating Killer Whale *Orca* species or subspecies is in the process of being described (R. Pitman pers. comm.), and a research programme on Antarctic Toothfish in McMurdo Sound has operated for about 30 years (deVries and colleagues, Eastman 1993). Data sets are developed enough that decadal and inter-annual variability has been identified in the physics (Jacobs & Giulivi 1998, Jacobs *et al.* 2002), the benthic communities (Dayton 1989) and the highest trophic levels (Testa *et al.* 1992, Wilson *et al.* 2001, Cameron 2001).

Measures of primary productivity and plankton standing stocks indicate the Ross Sea to be the richest area of water of comparable size in the entire Southern Ocean (Arrigo *et al.* 1998, 2002). Confirming this is the richness of benthic communities, which depend largely on the 'rain' of biotic particles from the surface (Dayton 1990). Surprisingly little research (here or elsewhere) has been conducted on the abundance and distribution of the important mid-trophic level forage species (Crystal Krill *Euphausia crystallophias* and Antarctic Silverfish *Pleuragramma antarcticum*), but the numbers of their top-trophic level predators also confirm the richness of the food web (see fig. 2). About 38% of the world population of Adélie Penguins *Pygoscelis adeliae* (940 000 of 2.5 million pairs) and 24% of Emperor Penguins

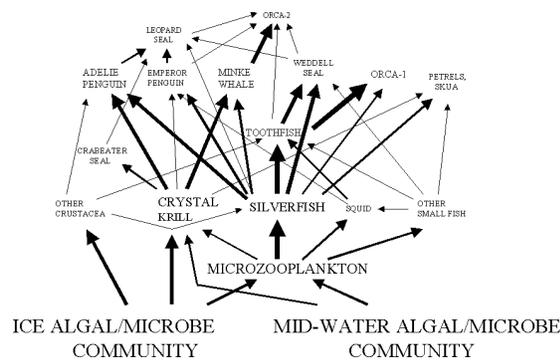


**Fig. 2.** Distribution of seabirds and cetaceans in the Ross Sea during December. Correspondence with the Shelfbreak Front (RSSlopeE) and the marginal ice zones are clear; large-scale ice edges shown by heavy dashed lines. Figure redrawn from Ainley *et al.* (1984).

*Aptenodytes forsteri* (52 000 of 215 000 pairs) breed along Ross Sea shores (Woehler 1993, Woehler & Croxall 1997). Of these Ross Sea populations, 93% of Emperor Penguins (year round) and 39% of Adélie Penguins (during summer) feed within the waters of the RSShelfE; the remainder feed in the RSSlopeE. Several million Antarctic Petrels *Thalassoica antarctica* feed within the RSSlopeE during summer, this being one of the greatest concentrations of this species anywhere in the Southern Ocean (Ainley *et al.* 1984, van Franeker *et al.* 1999). Some of these petrels are known to nest in Marie Byrd Land; but the breeding localities of the majority are not known. The unknown sites could be spread throughout all of West Antarctica, among the talus of nunataks and mountain tops hundreds of kilometres inland (van Franeker *et al.* 1999); almost all inland sites known have been discovered inadvertently by geologists seeking clues to other scientific questions. Similarly, among seals, Ross Sea numbers contribute the following to Pacific Sector populations at least as of the most recent surveys during the 1970s and early 1980s (cf. Stirling 1969, Gilbert & Erickson 1977, Ainley 1985): 45% of Weddell Seals *Leptonychotes weddellii* (32 000 individuals), 11% of Leopard Seals *Hydrurga leptonyx* (8000), and 12% of Crabeater Seals *Lobodon carcinophagus* (205 000). The difference in proportions is related to the fact that the last two species are much more pelagic (off shelf) than the neritic (continental shelf) Weddell Seal. Finally, of the order of 14 300 Minke Whales and 3500 Killer Whales *Orca orcinus* were estimated to occur annually within the

RSShelfE during the same time period (Butterworth & Best 1982, Ainley 1985). What the numbers of Minke Whales and their Killer Whale predators are now in the Ross Sea, Minke Whales having declined Antarctic wide (Branch & Butterworth 2001), remains to be determined.

Obviously, much about the Ross Sea is well known. The major gap in our understanding of the RSShelfE (and continental shelf ecosystems elsewhere in the Southern Ocean) is the coupling between lower and upper trophic components. In other words, how does the abundance and availability of middle-trophic level organisms respond to climate factors that, in turn, affect upper-trophic level populations, and *vice versa*? The two main middle-trophic-level species in the RSShelfE are Antarctic Silverfish and Crystal Krill (e.g. deWitt 1970, Hopkins 1987, Eastman 1993, Hubold & Hagen 1997, Pakhomov & Perissinotto 1997, Fig. 3). In Antarctic neritic waters these two species are the principal prey of all top-trophic species: Adélie and Emperor Penguins, Weddell Seals, Minke Whales and Antarctic Toothfish (Laws 1984, Eastman 1985, Ichii 1990, Plötz *et al.* 1991, Ainley *et al.* 1998, 2003a, Burns *et al.* 1998, Cherel & Kooyman 1998, Ichii *et al.* 1998, Davis *et al.* 1999). A soon-to-be-described 'new' Killer Whale preys on Antarctic Toothfish and possibly on Antarctic Silverfish. The Weddell Seal also preys on toothfish (Testa *et al.* 1985).



**Fig. 3.** A food web for the RSShelfE (neritic waters), emphasizing middle and upper levels. Pathways may differ on the basis of whether the base is composed of the ice-algal or mid-water algal community.

Also obvious is the simplicity of the RSShelfE, although many important interactions remain unknown (Fig. 3). Antarctic Silverfish and Crystal Krill are central, and interspecific competition for these organisms by upper trophic level predators is likely. The decrease or increase of any major species would likely elicit a demographic response in one of the others (e.g. Estes *et al.* 1998). Investigations of Adélie Penguin foraging currently underway around Ross Island indicate that these birds either deplete their prey or force it to become unavailable (through predator avoidance) during the period of penguin chick provisioning when foraging is most intense. The patterns observed have been: 1) a switch from one major prey (krill) to another (silverfish), 2) increasing foraging distance from colonies, 3) increasing foraging depth, and 4) increasing foraging time with food loads successively decreasing as well. Moreover, penguins from the largest colony, by their density, apparently exclude from their foraging area those penguins from nearby colonies (Ainley *et al.* 1998, 2000, 2003b, Ballard *et al.* 2001, 2002). During the chick-provisioning period, hundreds of Minke and Killer Whales also forage within the penguin foraging areas, but their influence on prey availability has yet to be investigated.

Prey depletion has also been observed among Weddell Seals in McMurdo Sound. These seals prey on Antarctic Toothfish during early spring, but apparently deplete these fish within breathing distance of the breeding areas where the seals concentrate. This was inferred from variation in human fishing success as a function of distance from seal haul outs (Testa *et al.* 1985). After depleting the toothfish, the seals turn to smaller prey, such as Antarctic Silverfish. Like all trophic interactions, other factors may also be involved in their persistence. For instance, confounding interpretation of these results is the lack of information on the movements of both the silverfish and the toothfish, independent of predator avoidance.

The RSSlopeE is another matter. There the dominant middle-trophic species is the Antarctic Krill *E. superba*. The natural history and role in food webs of Antarctic Krill is relatively well known. This organism has been the subject of intense research for 80 years, although not much effort has been expended on it in the RSSlopeE. Important to Antarctic Krill is the vertical movement of water along the shelf break. This species sheds its eggs in this region, depending on upwelling to assist the upward migration of

larvae. Besides this krill species, also important to upper trophic levels in the RSSlopeE, and elsewhere in deep waters of the Southern Ocean, are myctophid fish (Ainley *et al.* 1984, 1992). A provisional food web for these waters is presented in Ainley & DeMaster (1990).

## UNIQUE SCIENTIFIC VALUES

Nowhere else on Earth, other than perhaps the Weddell Sea and Hudson Bay, do we still have a natural laboratory in which can be observed a neritic marine ecosystem that has not been significantly affected by commercial fisheries or other human activity. Unlike other parts of the Southern Ocean, consistently collected data sets are long enough in the Ross Sea that clear patterns of decadal and inter-annual variability have been identified in the physics, the benthic communities, and the highest trophic levels. In such a well-defined but appreciably large system, these data sets have few parallels elsewhere in the Southern Ocean or even elsewhere on Earth. Questions remaining in regard to factors explaining identified trends in these ecosystem components will not be satisfactorily answered if exploitation of biological resources continues or expands in the Ross Sea. Decades of effort and expense will be lost, and like elsewhere, the climate-effect signal will be submerged by anthropogenic forces.

Thanks to long-term collections of data, decadal and ENSO-scale fluctuations in the weather, oceanography and sea-ice patterns of the Ross Sea have become apparent (Jacobs & Giulivi 1998, Jacobs *et al.* 2002). Within that context, periodic surveys along permanent transect lines in McMurdo Sound, begun by a series of researchers in the U.S. Antarctic Program (USAP) in the late 1960s, have identified a major shift in the composition of benthic communities that occurred during the late 1970s (Dayton 1989, 1990). The shift apparently is related to the formation of anchor ice. No such data have been gathered elsewhere in the Southern Ocean. Why the frequency of years of anchor ice formation has changed is not yet known.

The New Zealand Antarctic Programme (NZAP) has monitored the size of Adélie Penguin colonies on Ross Island annually since 1959 (Taylor & Wilson 1990). This data set is almost two decades longer than analogous ones elsewhere in the Antarctic (Woehler *et al.* 1999) and compares with any chronicle of seabird population change anywhere in the world. During the 1970s and especially the 1980s (to the present) the populations have been growing noticeably. Part of the variability (30%) in annual population size is related to sea-ice extent during winter (Wilson *et al.* 2001), but much more effort is required to understand the remaining factors affecting population change. Likely involved are changes in the formation and decay of sea ice and polynyas (D.G. Ainley, K. Arrigo, W.R. Fraser, A. Kato & P.R. Wilson unpubl. data). Within that context, the only existing demographic study of this species was completed by USAP researchers on Ross Island penguin populations during the 1970s, and a comparable study by USAP and NZAP is presently underway.

Finally, one of the longest demographic studies of a pinniped population anywhere, that of Weddell Seals, has been underway, first by NZAP and subsequently by USAP, in McMurdo Sound since the late 1960s (Stirling 1971, Testa & Siniff 1987, Testa *et al.* 1990, Cameron 2001). Initially, a take of seals to provide food

for dogs was allowed but has since been stopped (in the early 1980s) by agreement under the Antarctic Treaty. This population showed some major fluctuations in pups born and estimated numbers of adults in the early 1970s (Cameron 2001) but its size has remained relatively consistent since the mid 1980s. Why the population has become less variable remains to be determined; climate and food-web factors could well be involved.

## COMPETING SCIENTIFIC AND ECONOMIC INTERESTS

### Antarctic Toothfish

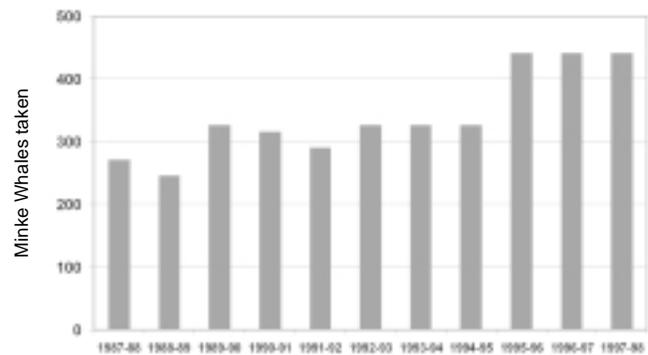
A fishery for Antarctic Toothfish has been developing in the RSShelfE during the past few years (Smith 2001, Waterhouse 2001). The potential of this fishing to affect the Ross Sea ecosystems is profound. The closely related Patagonian Toothfish *Dissostichus eleginoides* appears to have been severely over-exploited virtually everywhere that an industrial fishery has developed (Waterhouse 2001). Now those interests are looking at the Ross Sea.

Studies in McMurdo Sound, in which over 5000 Antarctic Toothfish have been caught, measured and tagged since the 1960s, reveal this to be a cornerstone species in the Antarctic ichthyofauna (Eastman 1985). Eastman characterizes this fish (along with its close relative, the Patagonian Toothfish), as 'the largest notothenioids and probably the most important piscine predators in the water column of the Southern Ocean' (p. 77). The Antarctic Toothfish reaches 163 cm total length and 60–70 kg in mass. Its growth is very slow (cm/year) and it reaches decades in age. Apparently, it spawns only every other year (A.L. de Vries pers. comm.). Recently, toothfish tagged in McMurdo Sound were caught near Cape Adare, 800 km to the north of McMurdo Sound. Therefore, the Ross Sea toothfish population travels widely. This species preys heavily on Antarctic Silverfish, as do most other top predators of the RSShelfE (Fig. 3). In turn, it is a major food of Weddell Seals and Killer Whales (see above).

Researchers working among the Aleutian Islands in the North Pacific Ocean have hypothesized that commercial fishing, principally for Walleye Pollock *Theragra calcogramma* (currently the largest fishery in the world) a trophically central species, has so altered the food web that Killer Whales are preying on Sea Otters *Enhydra lutris*, which is not the norm (Estes *et al.* 1998, Estes 2002). One result is that the reduction in Sea Otter numbers has led to a cascade of effects through benthic communities. Normally, otters control the populations of invertebrates (mainly sea urchins) that graze on seaweeds. Without the otters and, subsequently, without seaweeds, entire reef-dwelling fish communities have been negatively affected. This is an example of what could take place in the Ross Sea if the abundance of Antarctic Toothfish is significantly altered. Weddell Seal and Killer Whale populations either would have to decrease and/or increase their predation of other prey, including the whales taking more of the seals.

### Minke Whale

This species was exploited heavily in the Southern Ocean during the 1970s and 1980s, but this ceased in 1986 under an International Whaling Commission (IWC) moratorium. The take of the



**Fig. 4.** Minke Whales taken under a permit for scientific research in IWC areas V and VI, 1987–1997 (data from Brown & Brownell 2001). In 1990/91, 1992/93 and 1994/95, respectively, 79, 68 and 87 were taken from within the RSShelfE and, especially, RSSlopeE; of these 67%, 62% and 52% were pregnant females (Ichii *et al.* 1998).

Minke Whale had grown progressively as the other, larger baleen whales were over-exploited (Brown & Brownell 2001). Most of these Minke Whales were taken in IWC areas V (130°E–170°W) and VI (170°W–120°W), or that part of the Southern Ocean that includes the Ross Sea; more than 13 000 animals were taken during the first half of the 1980s. Because Area VI is mostly covered by pack ice year round at the latitude of the Ross Sea, and whaling vessels do not enter the pack ice, most of the catch came from the RSShelfE and RSSlopeE.

Since the moratorium went into effect, Japan has been permitting the take of this species in the Southern Ocean for scientific purposes as provided for in the International Whaling Convention, although this action has been questioned by many members of the IWC and its Scientific Committee (Brown & Brownell 2001, Clapham *et al.* 2003). About 80 whales, with more than half being pregnant females, have been taken annually within the Ross Sea, principally along the continental slope (i.e. the RSSlopeE; Ichii *et al.* 1998; Fig. 4). Therefore, several hundred Minke Whales have been taken from the relatively small area of the Ross Sea since the late 1980s and during a period of Minke Whale population decrease (see below).

Like the Antarctic Toothfish, Minke Whales live for decades and have a low reproductive rate (sexual maturity at 4–5 years of age; no more than one calf per year per mature female). The scientific take has been concentrated in IWC Areas V and VI (Ross Sea sector of the Southern Ocean), rather than being spread widely. Therefore, the 'local' impact potentially is great. Little is known about the persistence of local populations of this species. Like all the top predators, Minke Whales prey on Crystal Krill and Antarctic Silverfish in the RSShelfE, and on Antarctic Krill in the RSSlopeE (Ichii *et al.* 1998). The species is preyed upon extensively by Killer Whales (Mikhalev *et al.* 1981).

A single Minke Whale feeding twice daily consumes an estimated 21.5–33.8 tonnes (male and female, respectively) of food over three to four months in the Antarctic (Armstrong & Siegfried 1991). Some estimates are even higher. According to Ichii & Kato (1990), a single Minke Whale consumes 4% of body mass per day. This translates to 330 kg of food per day for females and 280 kg

for males. A single Adélie Penguin consumes about 0.9 kg per day during the chick-provisioning and subsequent pre-moult periods (Ainley 2002). Therefore, the removal of several hundred Minke Whales can have potentially important impacts on penguin foraging success. Adélie (and Emperor) Penguins from southern Victoria Land moult in the eastern Ross Sea (RSSlopeE) during February (Kooyman *et al.* 2000, Ainley 2002), at the time when the whale exploitation is underway in the RSSlopeE. The penguins are particularly voracious at that time, as they do not feed at all once the moult begins. Therefore, gathering adequate forage could well affect the subsequent survival of these penguins. Whether the penguins' population growth, and especially that since the mid-1980s (Wilson *et al.* 2001), is a consequence of more prey being available with a reduction of Minke Whale numbers is unknown, but this is certainly a possibility.

Rather enigmatic is the low body mass of Minke Whales, and especially pregnant females, taken from the Ross Sea (Ichii *et al.* 1998). Pregnant whales should be feeding voraciously. That being the case, Ichii *et al.* (1998) were at a loss to explain why these whales were so numerous in the Ross Sea, if foraging opportunities apparently were so poor. Because Killer Whales are also abundant, they reasoned that the Minke Whales would not be using the Ross Sea (and the sea ice so persistent there) in order to avoid predation (Killer Whales to a greater degree avoid pack ice). Ichii *et al.* (1998) however, did not entertain the idea that the whales could be avoiding whaling vessels.

The fact that Minke Whales have low body mass in the Ross Sea is a further indication – besides the prey depletion exhibited by Adélie Penguins and Weddell Seals – that the RSShelfE food web is sensitive to top-down forcing (see above). This is a concept difficult to fathom for most 'blue-water' marine biologists but, then, few have ever worked in a system where all the top-trophic predator populations are still robust. In systems without any top-down forcing, other than human fishing pressure, it is easy to assume that bottom-up forcing is the key to understanding food-web structure and population variations. Ultimately, then, the food web of the RSShelfE appears also to be very sensitive to perturbation. Loss of Minke Whales could well bring pressure for Killer Whales to seek alternate prey (even greater numbers of toothfish, seals, etc.), with consequent ecosystem repercussions.

## PLANNING FOR THE FUTURE

In marine ecosystems throughout the world, investigations and analyses are underway to determine how living resources can be managed sustainably in the context of increasing fishing pressure, rapidly changing climate, and other variables. A major problem is that most systems, other than the Ross and Weddell Seas and perhaps Hudson Bay, have been altered in uncertain and undocumented ways by decades and, in some cases, centuries of intensive human activities. Thus, it is difficult to differentiate the effects of natural variation from the cumulative effects of exploitation, climate change, point and non-point source pollution, etc. Effective fishery management remains a difficult challenge.

Continuing to investigate intensively and to monitor the few relatively unperturbed marine ecosystems, like the Ross Sea, which have been studied intensively and where we know that direct human influence has been minimal, can provide a body of infor-

mation that can be used to help predict the short-, mid-, and long-term effects of climate change and to identify and model alternative management strategies. For example, owing to interest in the history of the West Antarctic Ice Sheet, changes in the Holocene climate of few places on Earth are as well known as in the Ross Sea, as revealed in ice and sediment cores as well as the remains of marine creatures such as bivalves and penguins (e.g. Stuiver *et al.* 1981). Whereas we have learned a great deal about recent ecosystem structure and climate change in the Ross Sea during the past few decades, we have a long way to go before we can relate magnitude and sources of present-day natural variation to the Holocene record. To achieve this goal, we need to gather data through several more decades. The major gap remaining in our understanding of Ross Sea ecosystem functioning, as elsewhere in the world, are the processes that link trophic levels top down and bottom up. Unlike the rest of the world, however, our last chance to investigate these linkages, based on a huge platform of existing data, are in the Ross Sea.

CCAMLR, SCAR (Scientific Committee on Antarctic Research), IWC and the other authorities responsible for regulating and monitoring exploitation of living resources and other activities in the Ross Sea should consider what more might be done to assess and maximize the value of the Ross Sea as an 'ecosystem' laboratory.

## ACKNOWLEDGEMENTS

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## REFERENCES

- ACKLEY, S.F. & SULLIVAN, C.W. 1994. Physical controls on the development and characteristics of Antarctic sea ice biological communities – a review and synthesis. *Deep-Sea Research* 41: 1583–1604.
- AINLEY, D.G. 1985. The biomass of birds and mammals in the Ross Sea, Antarctica. In: Siegfried, W.R., Condy, P.R. & Laws, R.M. (Eds). Antarctic nutrient cycles and food webs. Berlin: Springer Verlag. pp. 498–515.
- AINLEY, D.G. 2002. Adélie Penguin: bellwether of climate change. New York: Columbia University Press.
- AINLEY, D.G. & DEMASTER, D.P. 1990. The upper trophic levels in polar marine ecosystems. In: Smith, W.O. (Ed.). Polar oceanography, Part B. New York: Academic Press. pp. 599–631.
- AINLEY D.G. & JACOBS, S.S. 1981. Affinity of seabirds for ocean and ice boundaries in the Antarctic. *Deep-Sea Research* 28A: 1173–1185.
- AINLEY, D.G., LERESCHE, R.E. & SLADEN, W.J.L. 1983. Breeding biology of the Adélie Penguin. Berkeley: University

- of California Press.
- AINLEY, D.G., O'CONNOR, E.F. & BOEKELHEIDE, R.J. 1984. The marine ecology of birds in the Ross Sea, Antarctica. *Ornithological Monographs* 32: 1–97.
- AINLEY, D.G., RIBIC, C.A. & FRASER, W.R. 1992. Does prey preference affect habitat choice in Antarctic seabirds? *Marine Ecology Progress Series* 90: 207–221.
- AINLEY, D.G., WILSON, P.R., BARTON, K.J., BALLARD, G., NUR, N. & KARL, B.J. 1998. Diet and foraging effort of Adélie Penguins in relation to pack-ice conditions in the southern Ross Sea. *Polar Biology* 20: 311–319.
- AINLEY, D.G., RIBIC, C.A., BALLARD, G., WILSON, P.R. & BARTON, K.R. 2000. Foraging-area overlap among neighboring colonies of Adélie Penguins: does competition play a role? Fourth International Penguin Conference Caja de Compensación de Los Andes, La Serena, Chile 4–8 September 2000. Books of Programme and Abstracts. p. 36.
- AINLEY, D.G., BALLARD, G., BARTON, K.J., KARL, B.J., RAU, G.H., RIBIC, C.A., & WILSON, P.R. 2003a. Spatial and temporal variation of diet within a presumed metapopulation of Adélie Penguins. *Condor* 105: 95–106.
- AINLEY, D.G., RIBIC, C.A., BALLARD, G., HEATH, S., GAFFNEY, I., KARL, B.J., BARTON, K.R., WILSON, P.R. & WEBB, S. 2003b. Geographic structure of Adélie Penguin populations: size, overlap and use of adjacent colony-specific foraging areas. *Ecology* in press.
- ANDERSON, J.B. 2000. Antarctic marine geology. London: Cambridge University Press.
- ARMSTRONG, A.J. & SIEGFRIED, W.R. 1991. Consumption of Antarctic Krill by Minke Whales. *Antarctic Science* 3: 13–18.
- ARRIGO, K.R., SULLIVAN, C.W. & KREMER, J.N. 1994. A simulated Antarctic fast-ice ecosystem. *Journal of Geophysical Research* C4: 6929–6946.
- ARRIGO, K.R., WEISS, A.M. & SMITH, JR, W.O. 1998. Physical forcing of phytoplankton dynamics in the western Ross Sea. *Journal of Geophysical Research* 103: 1007–1022.
- ARRIGO, K.R., VAN DIJKEN, G.L., AINLEY, D.G., FAHNESTOCK, M.A. & MARKUS, T. 2002. The impact of the B-15 iceberg on productivity and penguin breeding success in the Ross Sea, Antarctica. *Geophysical Research Letters* 29(7), 10.1029/2001GLO14160.
- BALLARD, G., AINLEY, D.G., RIBIC, C.A. & BARTON, K.J. 2001. Effect of instrument attachment and other factors on foraging trip duration and nesting success of Adélie Penguins. *Condor* 103: 481–490.
- BALLARD, G., AINLEY, D.G., ADAMS, J., BARTON, K., HEATH, S., HESTER, M.C., KARL, B.J., NEVINS, H. & WEBB, S. 2002. Adélie Penguin foraging behavior: variation depending on breeding season, colony, and individual. *Pacific Seabirds* 29: 30.
- BARRY, J. 1988. Hydrographic patterns in McMurdo Sound, Antarctica and their relationship to local benthic communities. *Polar Biology* 8: 377–391.
- BRANCH, T.A. & BUTTERWORTH, D.S. 2001. Southern Hemisphere Minke Whales: standardized abundance estimates from the 1978/79 to 1997/98 IDCR-SOWER surveys. *Journal of Cetacean Research and Management* 3: 143–174.
- BROWN, M.R. & BROWNELL, R.L. 2001. Review of catches of great whales taken in the proposed South Pacific sanctuary region. *International Whaling Commission /SC52/033*: 1–10.
- BURNS, J.M., TRUMBLE, S.J., CASTELLINI, M.A. & TESTA, J.W. 1998. The diet of Weddell Seals in McMurdo Sound, Antarctica, as determined from scat collections and stable isotope analysis. *Polar Biology* 19: 272–282.
- CAMERON, M.F. 2001. Dynamics of a Weddell Seal (*Leptonychotes weddellii*) population in McMurdo Sound, Antarctica. Unpublished PhD Dissertation, University of Minnesota, Minneapolis.
- CHEREL, Y. & KOOYMAN, G.L. 1998. Food of Emperor Penguins (*Aptenodytes forsteri*) in the western Ross Sea, Antarctica. *Marine Biology* 130: 335–344
- CLAPHAM, P.J., BERGGREN, P., CHILDERHOUSE, S., FRIDAY, N.A., KASUYA, T., KELL, L., KOCK, K-H., MANANILLA-NAIM, S., NOTABARTOLO DI SCIARA, G., PERRIN, W.F., READ, A.J., REEVES, R.R., ROGAN, E., ROJAS-BRACHO, L., SMITH, T.D., STACHOWITSCH, M., TAYLOR, B.L., THIELE, D., WADE, P.R. & BROWNELL, R.L., JR. 2003. Whaling as science. *BioScience* 53: 210–212.
- DAVIS, R.W., FUIMAN, L.A., WILLIAMS, T.M., COLLIER, S.O., HAGEY, W.P., KANATOUS, S.B., KOHIN, S. & HORNING, M. 1999. Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* 283: 993–996.
- DAYTON, P.K. 1989. Interdecadal variation in an Antarctic sponge and its predators from oceanographic climate shifts. *Nature* 245: 1484–1486
- DAYTON, P.K. 1990. Polar benthos. In: Smith, W.O. (Ed.). Polar oceanography, Part B. New York: Academic Press. pp. 631–686.
- DEWITT, H.H. 1970. The character of the midwater fish fauna of the Ross Sea, Antarctica. In: Holdgate, M.W. (Ed.). Antarctic ecology. London: Academic Press. pp. 305–314.
- DINIMAN, M.S., KLINCK, J.M. & SMITH, W.O. in press. Modeling Ross Sea circulation and biogeochemistry. Part I: Circulation dynamics. *Deep-Sea Research II*.
- EASTMAN, J.T. 1985. *Pleuragramma antarcticum* (Pisces, Nototheniidae) as food for other fishes in McMurdo Sound, Antarctica. *Polar Biology* 4: 155–160.
- EASTMAN, J.T. 1993. Antarctic fish biology: evolution in a unique environment. London: Academic Press.
- EL SAYED, S.Z. 1994. Southern Ocean ecology: the BIOMASS perspective. Cambridge: Cambridge University Press.
- ESTES, J.A. 2002. From Killer Whales to kelp. *Wild Earth Winter 2002–2003*: 24–28.
- ESTES, J.A., TINKER, M.T., WILLIAMS, T.M. & DOAK, D.F. 1998. Killer Whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282: 473–476.
- FRITSEN, C.H., LYTLE, V.I., ACKLEY, S.F. & SULLIVAN, C.W. 1994. Autumn bloom of Antarctic pack-ice algae. *Science* 266: 782–784.
- GARRISON, D.L., SULLIVAN, C.W. & ACKLEY, S.F. 1986. Sea ice microbial communities in Antarctica. *BioScience* 36: 243–250.
- GILBERT, J.R. & ERICKSON, A.W. 1977 Distribution and abundance of seals in the pack ice of the Pacific sector of the Southern Ocean. In: Llano, G.A. (Ed.). Adaptations within Antarctic ecosystems. Houston: Gulf Publishers. pp. 703–740.
- GROSSI, S., KOTTMEIER, S.T., MOE, R.L., TAYLOR, G.T. & SULLIVAN, C.W. 1987. Sea ice microbial communities. VI. Growth and primary production in bottom ice under graded snow cover. *Marine Ecology Progress Series* 35: 153–164.
- HOPKINS, T.L. 1987. Midwater food web in McMurdo Sound, Ross Sea, Antarctica. *Marine Biology* 96: 93–106.
- HUBOLD, G. & HAGEN, W. 1997. Seasonality of feeding and lipid content in juvenile *Pleuragramma antarcticum* (Pisces):

- Nototheniidae) from the southern Weddell Sea. In: Battaglia, B., Valencia, J. & Walton, D.W.H. (Eds). Antarctic communities: species, structure and survival. Cambridge: Cambridge University Press. pp. 277–283.
- ICHII, T. 1990. Distribution of Antarctic Krill concentrations exploited by Japanese krill trawlers and Minke Whales. *Proceedings of the NIPR Symposium on Polar Biology* 3: 36–56.
- ICHII, T. & KATO, H.H. 1991. Food and daily food consumption of southern Minke Whales in the Antarctic. *Polar Biology* 11: 479–487.
- ICHII, T., SHINOHARA, N., KUJISE, Y., NISHIWAKI, S. & MATSUOKA, K. 1998. Interannual changes in body fat condition index of Minke Whales in the Antarctic. *Marine Ecology Progress Series* 175: 1–12.
- JACOBS, S.S. & COMISO, J.C. 1989. Sea ice and oceanic processes on the Ross Sea continental shelf. *Journal of Geophysical Research* 94 (C12): 18195–18211.
- JACOBS, S.S. & GIULIVI, C.F. 1998. Interannual ocean and sea ice variability in the Ross Sea. In: Jacobs, S.S. & Weiss, R.F. (Eds). Ocean, ice and atmosphere: interactions at the Antarctic continental margin. *Antarctic Research Series* 75: 135–150.
- JACOBS, S.S., GIULIVI, C.F. & MELE, P.A. 2002. Freshening of the Ross Sea during the late 20th century. *Science* 297: 386–389.
- KOORYMAN, G.L., HUNKE, E.C., ACKLEY, S.F., VAN DAM, R.P. & ROBERTSON, G. 2000. Moulting of the Emperor Penguin: travel, location, and habitat selection. *Marine Ecology Progress Series* 204: 269–277.
- LAWS, R.M. 1984. Seals. In: Laws, R.M. (Ed.). *Antarctic ecology*, Vol. 2. London: Academic Press. pp. 621–715.
- MIKHALEV, Y.A., IVAHIN, M.H., SAVUSIN, V.P. & ZELENAYA, F.E. 1981. The distribution and biology of Killer Whales in the Southern Hemisphere. *Reports of the International Whaling Commission* 31: 551–566.
- PAKHOMOV, E.A. & PERISSINOTTO, R. 1997. Spawning success and grazing impact of *Euphausia crystallorophias* in the Antarctic shelf region. In: Battaglia, B., Valencia, J. & Walton, D.W.H. (Eds). Antarctic communities: species, structure and survival. Cambridge: Cambridge University Press. pp. 187–192.
- PLÖTZ, J., EKAU, W. & REIJNDERS, P.J.H. 1991. Diet of Weddell Seals *Leptonychotes weddellii* at Vestkapp, eastern Weddell Sea (Antarctica), in relation to local food supply. *Marine Mammal Science* 7: 136–144.
- SHERMAN, K., ALEXANDER, L.M. & GOLD, B.D. 1990. Large marine ecosystems: patterns, processes and yields. Washington, D.C.: American Association for the Advancement of Science.
- SHERMAN, K., ALEXANDER, L.M. & GOLD, B.D. 1993. Large marine ecosystems: stress, mitigation, and sustainability. Washington, D.C.: American Association for the Advancement of Science.
- SMITH, N. 2001. Letter to Hutchinson Kristan, *Antarctic Sun*, McMurdo Station, 21 November 2001.
- SMITH, W.O. & SAKSHAUG, E. 1990. Polar phytoplankton. In: Smith, W. (Ed.). *Polar oceanography*, Part B. London: Academic Press. pp. 477–525.
- STIRLING, I. 1969. Distribution and abundance of the Weddell Seal in the western Ross Sea, Antarctica. *New Zealand Journal of Marine and Freshwater Research* 3: 191–200.
- STIRLING, I. 1971. Population dynamics of the Weddell Seal (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica, 1966–1968. *Antarctic Research Series* 18: 141–168.
- STUIVER, M., DENTON, G.H., HUGHES, T. & FASTOOK, J.L. 1981. History of the marine ice sheet in West Antarctica during the last glaciation: a working hypothesis. In: Denton, G.H. & Hughes, T. (Eds). *The last great ice sheets*. New York: Wiley. pp. 319–369.
- TAYLOR, R.H. & WILSON, P.R. 1990. Recent increase and southern expansion of Adelie Penguin populations in the Ross Sea, Antarctica, related to climate warming. *New Zealand Journal of Ecology* 14: 25–29.
- TESTA, J.W. & SINIFF, D.B. 1987. Population dynamics of Weddell Seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. *Ecological Monographs* 57: 149–165.
- TESTA, J.W., SINIFF, D.B., ROSS, M.J. & WINTER, J.D. 1985. Weddell Seal–Antarctic Cod interactions in McMurdo Sound, Antarctica. In: Siegfried, W.R., Condy, P.R. & Laws, R.M. (Eds). *Antarctic nutrient cycles and food webs*. Berlin: Springer Verlag. pp. 561–565.
- TESTA, J.W., SINIFF, D.B., CROXALL, J.P. & BURTON, H.R. 1990. A comparison of reproductive parameters among three populations of Weddell Seals (*Leptonychotes weddellii*). *Journal of Animal Ecology* 59: 1165–1175.
- TESTA, J.W., OEHLERT, G., AINLEY, D.G., BENGTSON, J.L., SINIFF, D.B., LAWS, R.M. & ROUNSEVELL, D. 1992. Temporal variability in Antarctic marine ecosystems: periodic fluctuations in the phocid seals. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 631–639.
- VAN FRANEKER, J.A., GAVRILO, M., MEHLUM, F., VEIT, R.R. & WOHLER, E.J. 1999. Distribution and abundance of the Antarctic Petrel. *Waterbirds* 22: 14–28.
- VAN HEEZIK, Y. 1988. Diet of Adélie Penguins during the incubation period at Cape Bird, Ross Island, Antarctica. *Notornis* 35: 23–26.
- WATERHOUSE, E.J. (Ed.). 2001. Ross Sea region 2001: a state of the environment report for the Ross Sea region of Antarctica. Christchurch: New Zealand Antarctic Institute.
- WILSON, P.R., AINLEY, D.G., NUR, N., JACOBS, S.S., BARTON, K.J., BALLARD, G. & COMISO, J.C. 2001. Adélie Penguin population change in the Pacific sector of Antarctica: relation to sea-ice extent and the Antarctic Circumpolar Current. *Marine Ecology Progress Series* 213: 301–309.
- WOHLER, E.J. 1993. The distribution and abundance of Antarctic and Subantarctic penguins. Cambridge: Scientific Committee on Antarctic Research.
- WOHLER, E.J. & CROXALL, J.P. 1997. The status and trends of Antarctic and sub-Antarctic seabirds. *Marine Ornithology* 25: 43–66.
- WOHLER, E.J., COOPER, J., CROXALL, J.P., FRASER, W.R., KOORYMAN, G.L., MILLER, G.D., NEL, D.C., PATTERSON, D.L., PETER, H.-U., RIBIC, C.A., SALWICKA, K., TRIVELPIECE, W.Z. & WEIMERSKIRCH, H. 2001. A statistical assessment of the status and trends of Antarctic and Subantarctic seabirds. [Cambridge]: Scientific Committee on Antarctic Research.