

ACQUIRING A ‘BASE DATUM OF NORMALITY’ FOR A MARINE ECOSYSTEM: THE ROSS SEA, ANTARCTICA

CCAMLR document number: WG-EMM-04/20

1.0 SUMMARY.

The Ross Sea Shelf Ecosystem (RSShelfE) offers the last chance to understand ecological processes in a system where both top-down and bottom-up forcing are still intact. Elsewhere in Earth’s oceans the systems used for understanding ecological processes and fishery effects all have lacked significant, natural top-down forcing for such a long time that it is a concept rarely considered by researchers who currently investigate open-ocean systems. Herein, the importance of top-down forcing in pelagic and neritic marine ecosystems is reviewed with concrete evidence given for its existence in the current functioning of the RSShelfE. In spite of this unique evidence for the Antarctic region, much remains to be learned about cross-component interactions in the Ross Sea system. Should the RSShelfE be un-naturally altered, an easy accomplishment given increasing fishery pressure, we will have lost the last opportunity to understand the processes that take place in a healthy, complete marine ecosystem.

2.0 INTRODUCTION

“The practices we now call conservation are, to a large extent, local alleviations of biotic pain. They are necessary, but they must not be confused with cures. The art of [marine ecosystem] doctoring is being practiced with vigor, but the science of [ocean] health is yet to be born. A science of [ocean] health needs, first of all, a base datum of normality, a picture of how [a] healthy [marine ecosystem] maintains itself as an organism.” Adapted from Aldo Leopold (1949: p 196).

2.0.1 Incentive for this document. In 1996-97, commercial fishing vessels from New Zealand began to investigate the feasibility of catching Antarctic toothfish *Dissostichus mawsoni* in the Ross Sea, Antarctica. Operating under a quota established by CCAMLR (Convention for the Conservation of Antarctic Marine Living Resources) of 1,980 mt (CCAMLR statistical areas 88.1 and 88.2, south of 65° S), they landed <1 mt; four years later the experimental catch had grown to 751 mt (catch limit 2,340 mt; see CCAMLR 2002 and Figure 1). The experiment then ended. Each year following 1999, CCAMLR raised the catch limit, the number of countries sending vessels increased, and the catch rose; by 2003-04 the limit was set at 3,625 mt. With the number of countries participating increasing sharply to 10 (> 20 vessels), 2003-04 may be the first year that the legal quota will be realized. The illegal take will be more than triple that catch (Hutchison 2004). Assuming an average mass of 50 kg per fish, the 2003-04 quota represents a take of 75,000 voracious predatory fish that are up to 50 years old, slow to grow and mature, slow to be replaced (Horn 2002), and key to the Ross Sea Shelf Ecosystem (RSShelfE) (see below, also CCAMLR 2002). At the same time, beginning in 1987 and continuing to the present, Japanese whalers have been killing minke whales *Balaenoptera bonarensis*, on the order of 400 adults per year, in a scientific experiment also in the Ross Sea. This

species, too, is slow to grow and mature (Brown & Lockyer 1984, Ohsumi & Masaki 195), and also is key to the functioning of the RSShelfE (see below). Meanwhile, marine biologists from at least four Antarctic Treaty nations, in an effort requiring many thousands of person hours and many millions of dollars (US), have conducted their research in the RSShelfE and vicinity under the assumption that large- and meso-scale variation in the patterns they observed was due to climate and other natural forcing (see CCAMLR 2002, Ainley 2002a). The work on climate change effects on the ecosystem, from the present back through the entire Holocene and beyond, has been deemed to be of global importance.

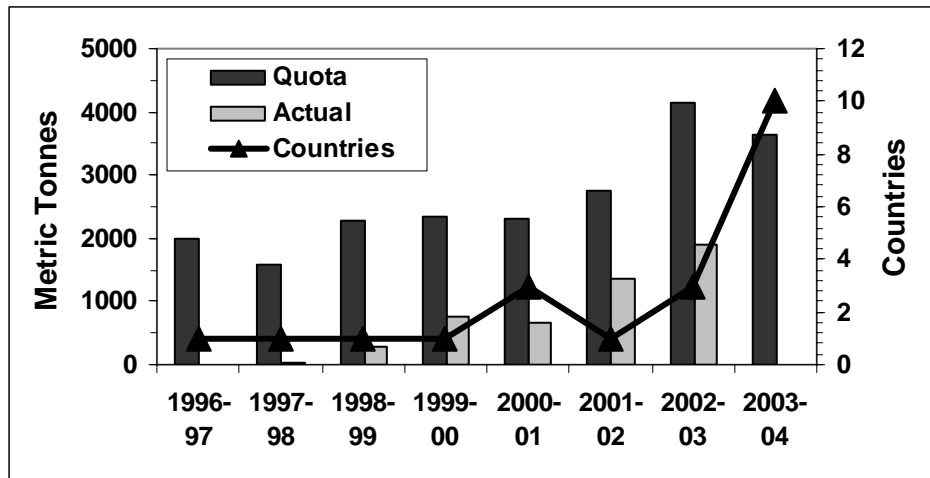


Figure 1. A summary of industrial fishing effort for Antarctic toothfish in the Ross Sea (FAO areas 88.1 and 88.2, south of 65° S). Shown are the CCAMLR quotas, the actual catch, and the number of countries whose vessels are participating.

Contemporary with these fisheries, in 1998, the U.S. National Science Foundation organized an international panel of experts to assess the progress and future of marine biological research as judged at the end of the 20th century. Among the very first lines of text in their report, called OEUVRE (Ocean Ecology: Understanding and Vision for Research), was the following statement (NSF 1998, p 1): “A more sobering discovery is that little if any of the ocean remains unaffected either directly or indirectly by fisheries, agricultural runoff, sewage, aquaculture and industry.” The report goes on with examples of how these factors have irreparably altered the marine portion of our planet. While the Ross Sea has escaped all those factors thus far (CCAMLR 2002), the effects of fishery extraction are now threatening the RSShelfE, heretofore, as noted, a sanctuary for international ecological marine research. The OEUVRE report went on to detail newly discovered evidence that top down forcing, the first processes to be effected by fishing extraction, should be looked at more seriously in investigations of open-ocean marine ecosystems.

2.0.2. *Why consider the Ross Sea?* Argued very well by D Pauly & J MacLean (2003), in their analysis of the state of the North Atlantic Ocean, is the point that biologists, assuming the responsibility to assess trophic pathways, processes and community

structure in marine ecosystems, have been dealing with a moving target over the past century or more. Fisheries have so depleted, and are continuing to rapidly deplete, the upper and middle trophic levels of almost all the World's oceans that the definitions of a 'healthy' marine ecosystem, normally functioning trophic pathways, and the management targets to achieve them, in reality, no longer apply. Pauly & MacLean recount 17th-century descriptions of marine life from the western Atlantic that are not believable now — whales so numerous to impede ship traffic, cod 1-2 m long as numerous as grains of sand, shellfish the size of dinner plates reprocessing the waters of large coastal estuaries in a matter of days, and so on. All that and more has been gone for a long time. For several generations, the information that marine scientists and fishery biologists have been amassing has been collected from broken ecosystems, no longer having any top-down forcing other than fishery pressure. Aldo Leopold's words (above), directed at the time toward a land-use management, therefore, are acutely appropriate for the ocean in the present era (see, e.g., Myers & Worm 2003). In the first decade of the 21st century, we have but one, in the true sense of the word, 'healthy' open-ocean marine ecosystem remaining on Earth, and within it alone do we still have a final chance to gauge how such marine ecosystems should function in the face of rapid climate change.

The one marine ecosystem remaining, and located literally at the 'end of the Earth,' is that of the Ross Sea continental shelf ecosystem (RSShelfE). This ecosystem lies west of 155° W and in waters shallower than 3000 m; it is an area about the size of southern Europe (CCAMLR 2002, Ainley 2002a), comprising perhaps 5% of the Southern Ocean. The Ross Sea's distance from civilization and its often brutal environment heretofore have provided protection from over-exploitation of its biotic resources. In recent years, however, as noted above, minke whale and toothfish fisheries have discovered the Ross Sea's untapped richness. In a scenario that has been repeated countless times before but elsewhere on the watery portion of the globe (e.g., Pauly et al. 1998, Myers & Worm 2003), we may now be on the brink of forever losing that last ecosystem standard unless its value as a 'base datum of normality' is recognized. Not only recognized, as has been the case already (CCAMLR 2002), but efforts made as well to shift fishery exploitation elsewhere. Otherwise, reconstruction of healthy marine ecosystems for all places on the globe will be reduced entirely to computer models (e.g. Myers & Worm 2003).

Already, in other portions of the Southern Ocean — in the 'Antarctic marine ecosystem' (i.e., the system referred to and described by Laws 1977, May et al. 1979, Hempel 1985, and others) — industrial fisheries, as elsewhere, have changed the ecosystem profoundly, and likely irreversibly, in a practice called, "Fishing down the food web." As detailed by Pauly et al. (1998), the fishery catch in major portions of the 'Antarctic marine ecosystem' has already declined more than one trophic level, from an average of about 3.4 to < 2.4 during the past 30 years (mostly pre-CCAMLR) as insular shelf stocks of benthic fishes have been severely depleted (Figure 2). In those ecosystems only the fishing for Antarctic krill *Euphausia superba* remains. The measured drop in trophic level is huge in a part of the world renown for its very short food-chains (El Sayed 1994, Knox 1994). Moreover, according to theory, a one trophic-level change in

food chain length is exactly that needed to fundamentally alter the workings of a food web (Hairston & Hairston 1993, Fretwell 1987).

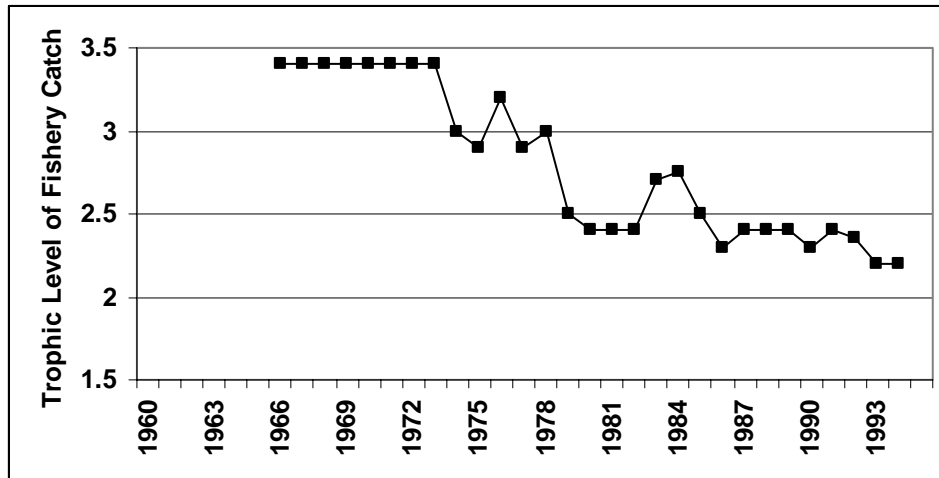


Figure 2. The trophic level of the fishery catch in FAO areas 48, 58 and 88; redrawn from Pauly et al. (1998).

Over the past 100 years, the process of removing all organisms of the upper trophic levels (except man) from marine ecosystems has been very effective (e.g., Pauly et al. 1998, Jackson et al. 2001, Pauly & MacLean 2003). Presently at the top are the former middle trophic levels, the organisms of which, with their exceedingly short life-cycles (days, weeks, to a few years), are able to respond quickly to the weather- and climate-induced vagaries of nutrient input and phytoplankton production (e.g., Anderson & Piatt 1999, Batchelder et al. 2001, Walther et al. 2002). Upper-trophic level organisms, however, owing to their long lives and delayed onset of maturity exhibit various lags in response, living through times of depleted prey (often forgoing reproduction) and cropping them down (and reproducing) in times of plenty. Where top down control is still important, modest changes in primary production would have very little effect on populations at higher trophic levels. Oscillations in abundance at middle trophic levels might well be dampened as well (Post et al. 2000).

In the case of the RSShE (described in CCAMLR 2002), which is distinct from the ‘Antarctic marine ecosystem,’ while phytoplankton production is important and well studied, we are still at a point where top-down forcing, although yet to be properly researched, is equally important in the functioning and structure of its food webs and communities, i.e. top predators have as much influence on energy flow in the entire foodweb as does phytoplankton production (see below). Indeed, waters of the RSShelfE are more productive than any other stretch of the ocean south of the Polar Front (Arrigo et al. 1998), a phenomenon reflected, in part, by the immense populations of its ‘charismatic megafauna,’ such as penguins, whales and seals, and the healthy food web of which these are a part (CCAMLR 2002). Still existing in the RSShelfE are conditions similar to what Pauly & MacLean describe of the former North Atlantic Ocean.

3.0 EVIDENCE FOR TOP DOWN FORCING OF COMMUNITY PATTERNS IN MARINE ECOSYSTEMS, INCLUDING THAT OF THE ROSS SEA SHELF

In terrestrial, freshwater and intertidal/shallow-subtidal ecosystems the healthy growth of plant or algal life occurs where sunlight and nutrients (and, in the case of land systems, moisture) are plentiful. Such growths then attract robust communities of grazers and, in turn, the less abundant predators of those grazers, the so-called ‘charismatic megafauna.’ Such a chain of nutrient transfer is known to ecologists as ‘bottom up forcing’ of community and food-web structure (i.e., defined as the numbers of organisms at each step in food chains/webs, who eats whom, where and when, and the efficiency of nutrient transfer). It is also known, if only recently and perhaps only by ecologists, that if one removes the top predators — for example, the wolves, predatory fish and sea otters — the entire system changes dramatically even to its basal nutrient components (e.g. Brown & Heske 1990; Carpenter & Kitchell 1987; Carpenter et al. 1987; Dayton 1985; Estes et al. 1978, 1989; McLaren & Peterson 1994; Power 1984, 1990; Power et al. 1985). The latter result indicates ‘top-down forcing’ of community and food-web structure. Obviously, in healthy ecosystems both types of forcing play a role in structuring biotic processes.

Until very recently, it has been a maxim among marine ecologists that top-down forcing could never be a major element of pelagic or extensive neritic ecosystems, as the latter are just too large and the physical forcing just too strong for top-down processes to express themselves (OEUVRE 1998). Given the state of the world’s oceans, depleted long before science attained the capability to precisely quantify open-ocean ecological relationships (see below), we may never really know the degree to which this is true. However, evidence is now emerging to show that top-down processes indeed can have profound effects on the community structure and trophic transfer in pelagic ecosystems (e.g., Eiane et al. 2002, Estes et al. 1998, Ohman et al. 2004, Pace et al. 1999, Shiomoto et al. 1997, Springer et al. 2003, Worm & Myers 2003, Verity & Smetacek 1996, Tynan 2004). Formerly, before top and near-to-top predators were removed from marine ecosystems, top-down forcing had far more influence than it does now (Pauly & MacLean 2003).

In spite of its remote location and the challenge of conducting science in its harsh environment, an amazing amount of marine physical and ecological research has been conducted in the Ross Sea. This has been the result of efforts within three national Antarctic programs (Italy, New Zealand, USA) over the past 30 years (reviewed in CCAMLR 2002). A number of the longest time series of marine biological and marine climatic data in the Antarctic are part of this record (see www.penguinscience.com, LTER Workshop for a bibliography of over 700 titles). Most of the work has been conducted by individual or small-groups of investigators, with multi-national efforts such as AMLR, BIOMASS, GLOBEC and CCAMLR-EMM being conducted in those parts of the Southern Ocean, the ‘Antarctic marine ecosystem,’ where research vessels can proceed without having to contend with sea ice during at least part of the year.

Other than phytoplankton production, biogeochemical cycling and control of benthic systems (e.g., Dayton 1990, Dayton et al. 1992, DeMaster et al. 1992, Barry et al.

2003, DiTullio & Dunbar 2003), there has yet to be much synthesis of the processes that contribute to the remainder of the RSShelfE. Knowledge of the Ross Sea's middle trophic levels is woefully incomplete, as it is for other continental shelves of Antarctica. Nevertheless, enough detailed work has been conducted that evidence is available to indicate a different fauna than that of the 'Antarctic marine ecosystem' as well as the existence of important top-down forcing (i.e., downward effects of predation pressure on the availability and distribution of middle-trophic-level species). While the following observations are somewhat anecdotal, no similar observations have been forthcoming from other parts of the Southern Ocean, perhaps because the top-trophic species long have been effectively removed or severely reduced.

- Adélie penguins *Pygoscelis adeliae*, especially those at one of the largest existing colonies for this species (Cape Crozier, Ross Island), must feed farther from colonies and deeper in the water column as the summer passes (Ainley et al. 2003; Ballard et al. unpubl.; Figure 3). This is evidence that these predators may be depleting their prey or altering their availability.

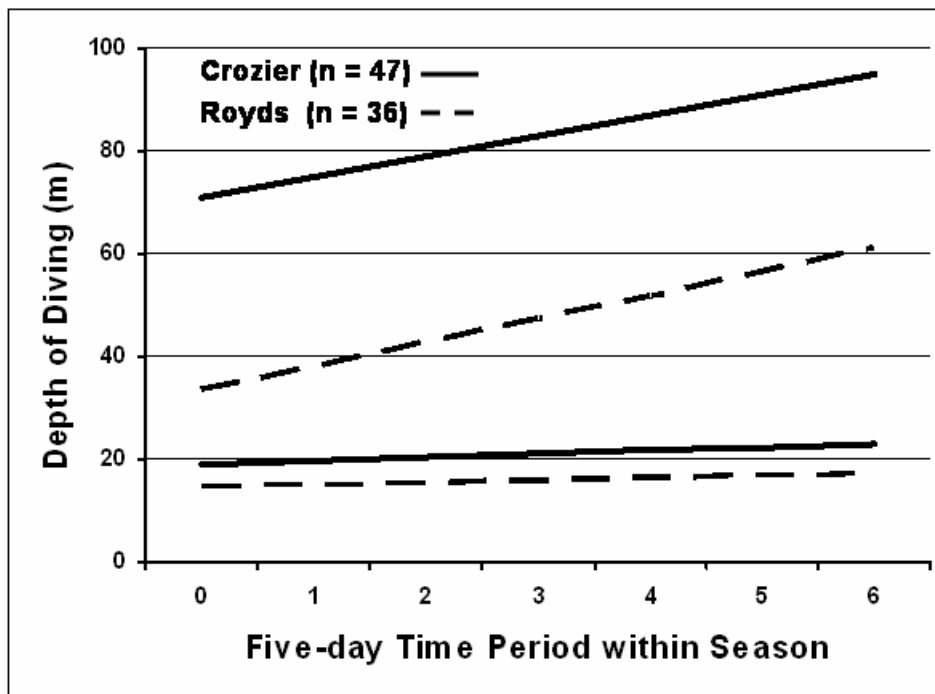


Figure 3. Mean and maximum diving depths for breeding Adélie penguins at Cape Crozier and Cape Royds, 1999-00 to 2001-02 (only 2 years for Royds). Data shown are predicted values from 2-way linear model controlling for effects of seasonal variation. Dive depths increased as breeding seasons progressed (all $P \leq 0.02$). Sample sizes are numbers of individuals.

- The effort of Adélie penguins to find food in the Ross Sea is affected negatively by the feeding of minke whales and 'type C' killer whales *Orcinus orca*. After the arrival of these whales in the penguins' foraging area, the penguins have to feed

farther away (Ballard et al. unpubl. data; Figure 4). This is evidence, too, that together these predators are depleting or affecting the distribution of middle-trophic level species at a scale of 100s of km².

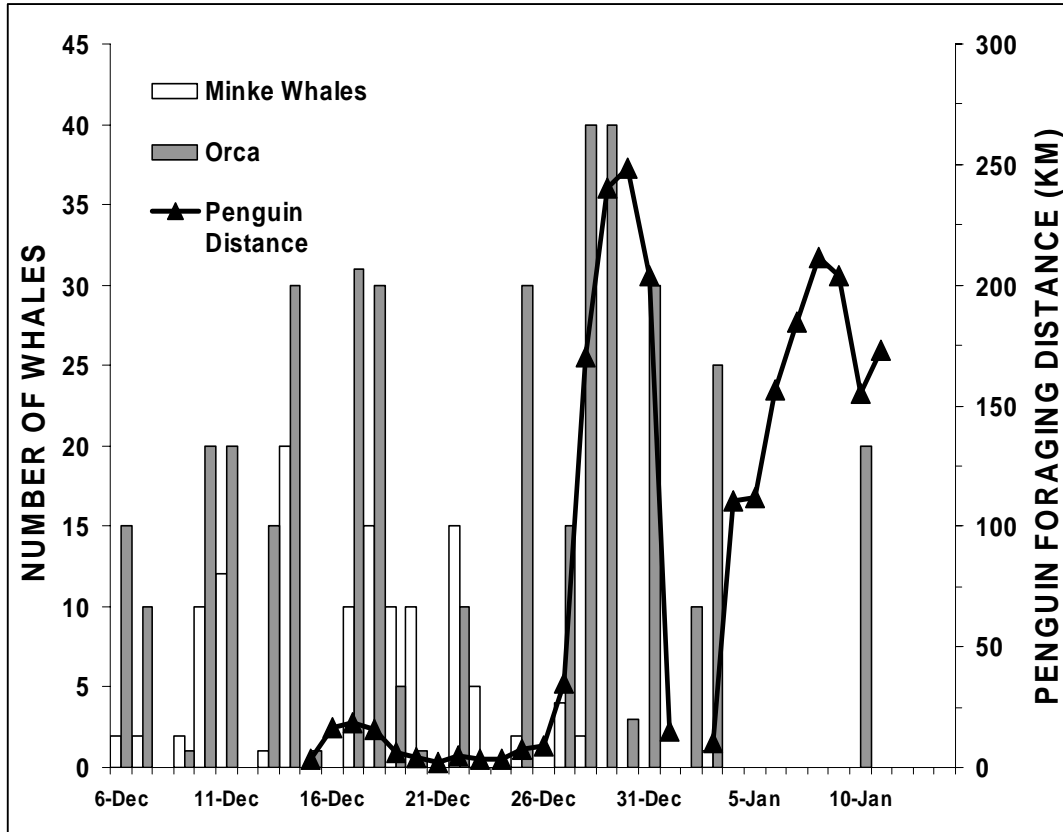


Figure 4. The number of minke and killer whales (type ‘C,’ *O. glacialis*; a fish-eating form; Pitman & Ensor 2003) feeding in sight of Cape Crozier, Ross Island (logged daily, visibility permitting), and the length of foraging trips by Adélie penguins provisioning chicks at Cape Crozier (Ballard & Ainley, unpubl. data). The penguins, present since late October, initially feed (on fish) very close and among the whales, with longer trips when more whales are present. Eventually the penguins must feed elsewhere; soon thereafter the whales, especially minkes, disappear from the area as well. The implication is that all these predators have depleted the food supply. Penguin foraging distance was determined by satellite telemetry, which began in mid-December with the start of chick-provisioning.

- Minke whales, feeding along fast-ice edges, attempt to break breathing holes further in from the edge in order to extend their access to food, which apparently has been depleted in the open water and just back from the ice edge (Figure 5). These holes initially are a boon to foraging penguins, also excluded from prey by the fast ice (Ainley 2002b). Predation along the ice edge likely results in a zone depleted of prey, as observed in the Weddell Sea where it was ascribed to the productivity characteristic of large-scale ice edges as well as predation (Brierley et al. 2002).

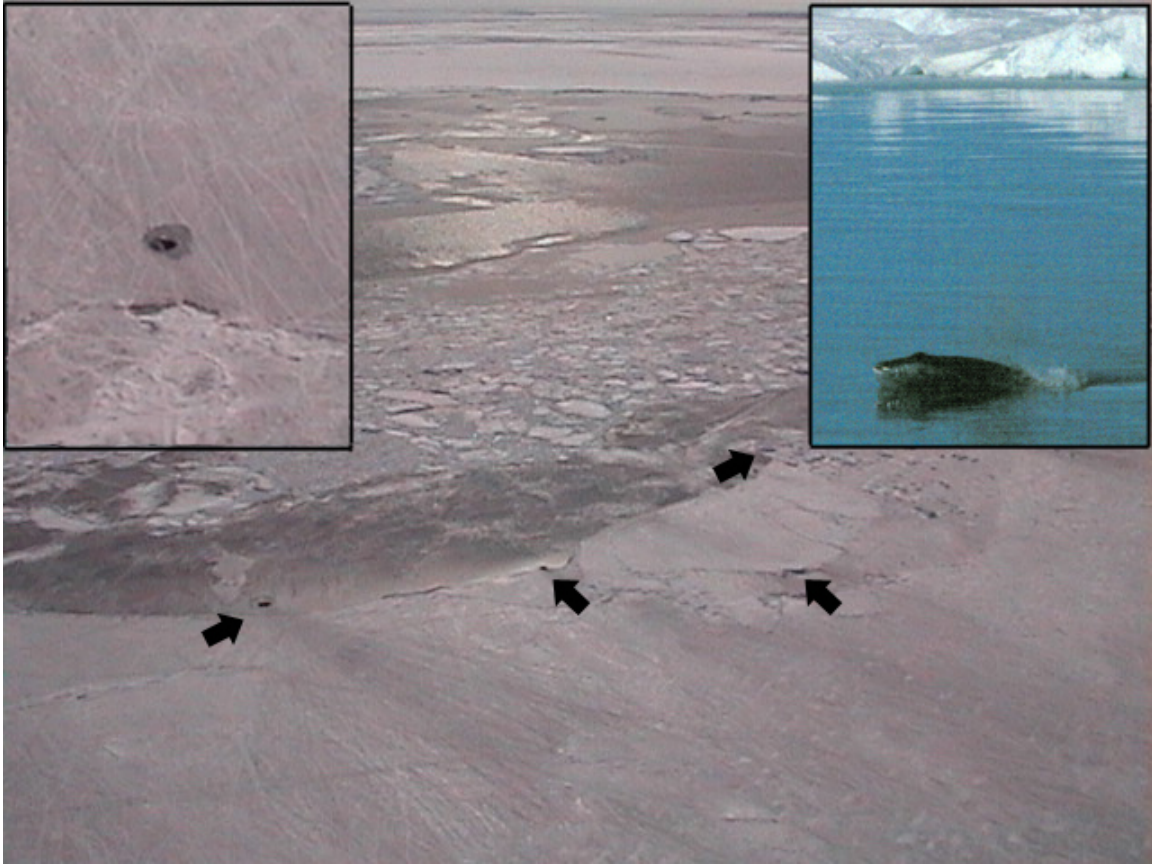


Figure 5. Aerial view of fast ice edge in McMurdo Sound, Ross Sea, showing holes punched by minke whales (inset right, minke whale breaking through 'new' ice); December 2001.

- Weddell seals *Leptonychotes weddellii* feed so heavily on Antarctic toothfish (Figure 6) that they deplete the fish in the vicinity of the seal haulouts, as indicated by catch-per-unit effort of long-lines (Testa & Siniff 1985). Recent observations of food (fish) hoarding by Weddell seals (i.e., defending stored fish, as observed by divers; S. Kim et al. ms; Figure 7) indicate further that prey depletion is a factor affecting this seal species, which for much of the year (adults at least) must remain within range of sea-ice tide cracks, needed by the seals for breathing and access to the upper surface of the ice.

For decades biologists have reported seals, rising on occasion with a toothfish in their mouths in the ice holes drilled to conduct scientific activities in McMurdo Sound (e.g., Calhaem & Christoffel 1969). In 2001-02 and 2002-03, the Sound was covered by fast ice far more extensively than normal (fewer cracks), and seal numbers were low as a consequence. Killer whales (another toothfish predator), as well, were deprived access of waters that usually become ice free in the late summer (see below). In 2003-04, when the fast ice finally retreated to its usual extent, allowing the expected intrusion of seals, scientists reported seals surfacing with a toothfish 1-3 times daily for weeks. Seemingly, the extensive fast ice had offered protection of toothfish from predation, and toothfish numbers had subsequently grown; or, more likely, that the toothfish were attracted to an increased abundance of silverfish, as other forage species, which

themselves have enjoyed protection from the predation by seals, whales and penguins.



Figure 6. A subadult Weddell seal that has brought a toothfish, about a third of its own size, into a hole made by researchers for their access to the water column; photo Justin Heil, McMurdo Sound, November 2003.



Figure 7. A Weddell seal that had temporarily ‘stored’ uneaten portions of a toothfish on the bottom of McMurdo Sound, and who now is removing the remains from the reach of research divers (S Kim et al. ms). Frame grab of a video sequence; ©Rob Robbins).

- Icebreakers, making a channel through the McMurdo Sound fast ice in order that cargo ships can re-supply McMurdo Station and Scott Base, are followed by the fish-eating form of killer whales, ‘type C.’ These predators use the channel to reach toothfish; until the channel is forged, the extensive fast ice protects the fish from predation (Figure 8). Seemingly, the fish had been depleted seasonally from waters within breath-holding distance of the ice edge. The channel also usually loosens the fast ice of McMurdo Sound and this usually leads to a large scale break out. This did not occur during 2001-02 or 2002-03, when the ice was unusually thick (see above, Weddell seal discussion).

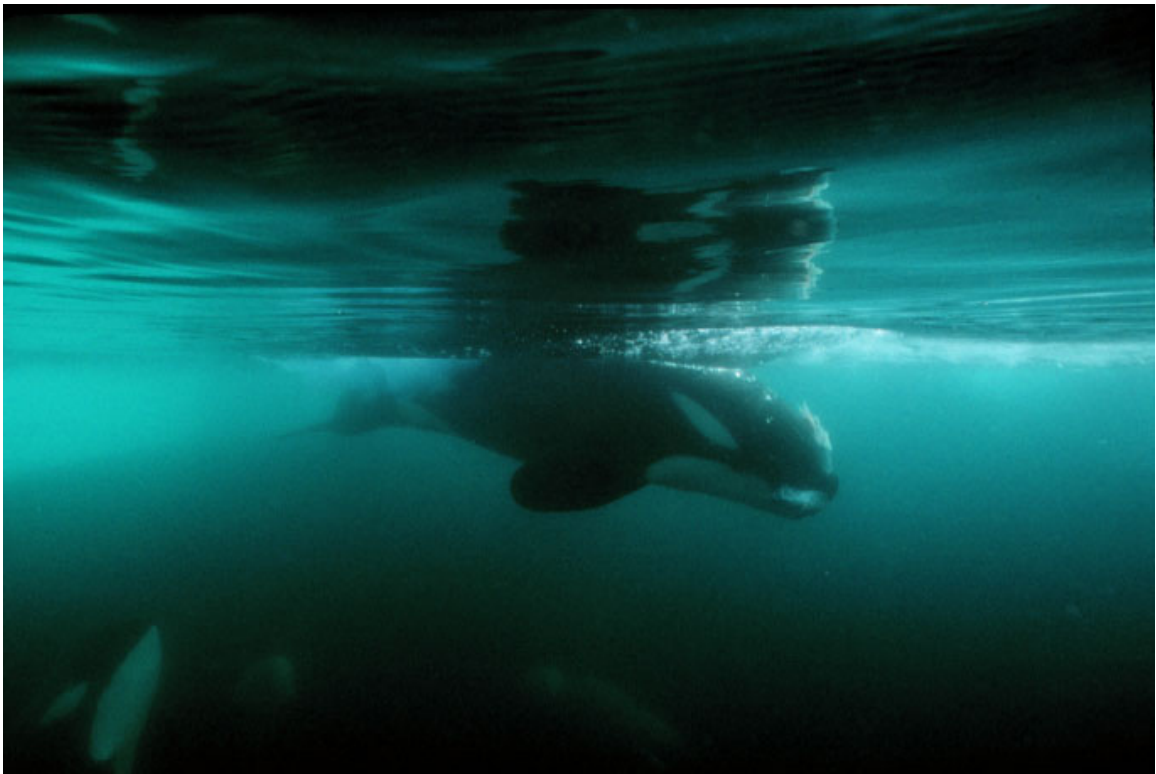


Figure 8. A killer whale (type ‘C’) at the fast ice edge of McMurdo Sound, with a toothfish in its mouth (the fish’s head protrudes from the right side of the whale’s mouth; the fish’s tail, stripped of skin, protrudes from the opposite side); photo © Norbert Wu.

- The density and distribution of benthic invertebrates in shallow-water McMurdo Sound communities, such as starfish and urchins, may well be affected significantly by the input of food (toothfish carcasses, etc) dropping from the tide cracks used by Weddell seals for air and food access (S. Kim, pers. comm.). Weddell seals do not eat toothfish heads, the toothfish skin, nor filleted remains of toothfish dumped by researchers (K Hoefling, pers. comm.). These tissues drop to the ocean floor where they are immediately consumed by other organisms. Therefore, the availability of toothfish to the seals affects the organization of the benthic invertebrate community in shallow waters like those in McMurdo Sound (Figure 9).



Figure 9. Left, the clumping of sea stars (*Odontaster validus*) on a hunk of organic detritus that fell from a tide crack and, right, sea stars attracted to an experimental food source, both in McMurdo Sound, Antarctica; photos S. Kim.

The above are examples of how top-trophic predators, because of their abundance and behavior, are able to quickly deplete the availability or change the distribution of middle-trophic organisms (prey) in the RSShelfE, and how predation by top-trophic predators in surface waters indirectly provides an important food source for benthic organisms. Virtually all of the RSShelfE's top-trophic and charismatic megafauna — all seals, whales, seabirds (including penguins, and toothfish — have a diet composed principally of the same two middle-trophic level species, the Antarctic silverfish *Pleuragramma antarcticum* and crystal krill *Euphausia crystallophias*. Killer whales (type 'C') and Weddell seals also feed, and at times principally, on Antarctic toothfish, (reviewed in CCAMLR 2002; Figures 6-8, 10). Therefore, the potential for intra- and interspecific trophic competition is high and perturbation of the system by removal or severe reduction of even one upper- or middle trophic level species, e.g. minke whales and toothfish, is likely to have marked repercussions. Both the mid-water and benthic communities would be noticeably changed. As assessed by D Strong (1992), therefore, the Ross Sea meets the criteria of a system that can provide what are called 'trophic cascades' or effects exerted downward on lower trophic species and levels by top-trophic, and especially 'keystone,' predators. First, the RSShelfE is physically contained, it being largely a bay located south of the Antarctic Divergence or East Wind Drift (and therefore with much recirculation of its own waters; see figure in CCAMLR 2002); and, second, its food web is very simple with relatively few species involved (Figure 10). In fact, the frequency of trophic cascades, or the propensity for them to occur may be more widespread than argued by Strong (Pace et al. 1999).

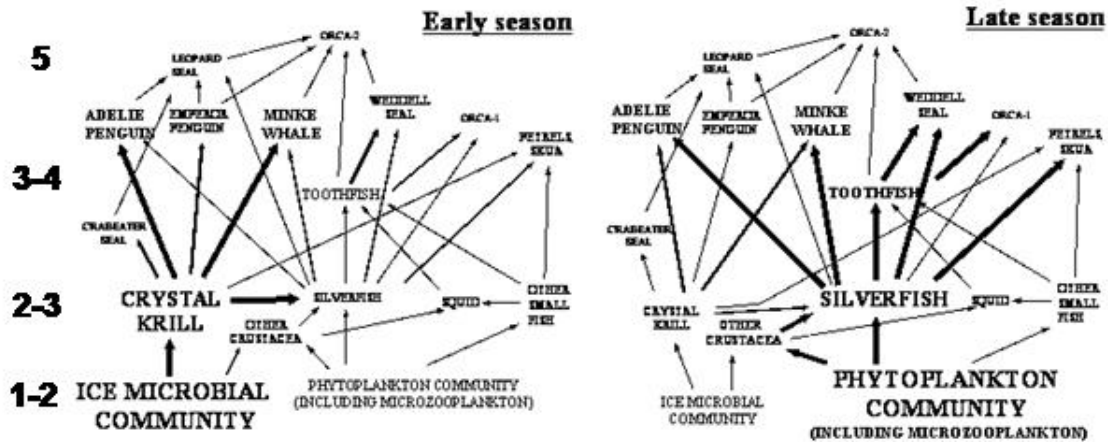


Figure 10. Flow diagram of the McMurdo Sound food web, with emphasis on middle- and upper-trophic levels. During the early season much sea ice is present and the input of the sea-ice microbial community is important; during the late season open waters prevail and water-column processes become dominant. Numbers along the left provide an estimate of trophic level. ‘Orca-2’ is actually types ‘A’ and ‘B’; orca-1 is type ‘C’ (see Pitman & Ensor 2003).

4.0 MANAGEMENT OF MARINE RESOURCES IN A TOP-DOWN AND BOTTOM-UP FORCED SYSTEM

The signatory countries under the Antarctic Treaty regulate and closely monitor the ‘footprints’ left by scientific and commercial activities on the Antarctic continent; in fact, these countries are constantly trying to reduce impacts (e.g., Kuenning & Hutchison 2003). Minerals extraction on the continent and in the waters surrounding it is not allowed under a recent agreement. The Treaty, on the other hand, abrogates responsibility for the management of marine living resources south of the Antarctic Polar Front to the International Whaling Commission (IWC), in the case of cetaceans, and CCAMLR, in the case of other fisheries.

Under the IWC, a ‘research’ project on minke whales is being conducted by scientists from Japan in the outer Ross Sea and Ross Sea continental slope; the project since 1987 has been centered on the killing of ~400 minke whales per year (Ichii et al. 1998, Brown & Brownell 2001; see summary in CCAMLR 2002). Before this research began, during the previous two decades, commercial whaling removed many thousands of minke whales from the sector of the Southern Ocean that includes the Ross Sea (Figure 11). Given this species’ demographic parameters (Brown & Lockyer 1984), its Antarctic population could not withstand the earlier commercial take and for that reason the commercial whaling was halted. To date, no direct assessment of the ecosystem effects of whale extraction has been part of any cetacean research project in the Antarctic, although the theoretical implications have been well discussed for the portion referred to as the ‘Antarctic marine ecosystem’ (e.g., Laws 1977, May et al. 1979; see Springer et al. 2003 for possible effects on the northern North Pacific caused by industrial whaling).

Given that top-down forcing is important in the RSShelfE, as reviewed herein, this minke whale project, coming on the heels of the commercial whaling, has potentially affected the results of all other marine ecological research in the Ross Sea during recent decades. The consumption of prey by *one* minke whale during its summer and autumn feeding in the Ross Sea is equivalent to what would be taken by a *few thousand* Adélie penguins (cf. Ichii & Kato 1991, Woehler 1995). Both species are denizens of the pack ice and adjacent areas (see above, Figure 4), and occur together where the whale study is being conducted (late summer/autumn, mostly eastern Ross Sea). Adélie penguin populations in the Ross Sea increased dramatically during the period of the commercial take of minke whales, a trend that leveled when the commercial take ended and the scientific one began (Figure 11).

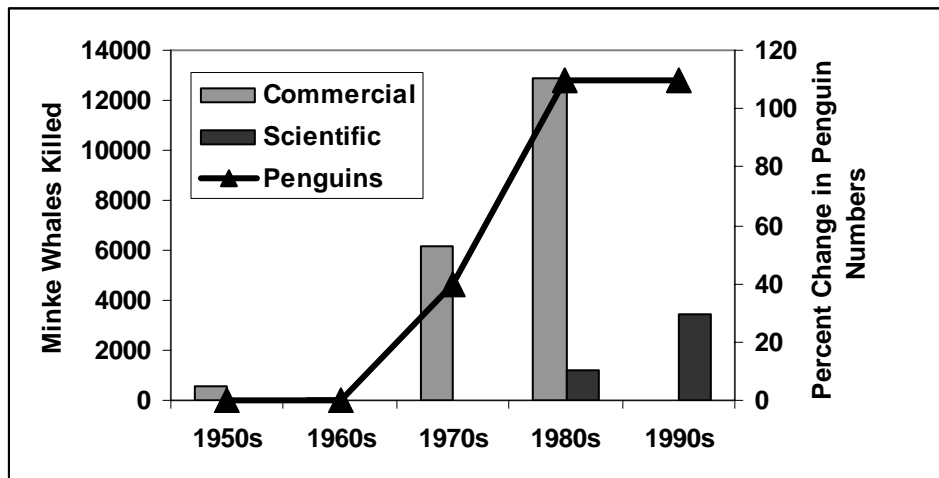


Figure 11. Percent change by decade in the numbers of Adélie penguins breeding at capes Royds and Bird, Ross Island, Ross Sea, and the take of minke whales in IWC areas V and VI (Ross Sea sector). These penguins spend the late summer, autumn and winter in the area from which minke whales have been removed annually by the commercial and scientific take, also during the late summer and autumn. Data on penguins from Wilson et al. (2001); those for whales from Brown & Brownell (2001).

On the one hand, at least from an Antarctic-wide perspective, the minke whale population as of recent years has returned to its pre-exploitation level (Branch & Butterworth 2001). This should reduce or reverse the penguin increase, if, in fact, the relationships referred to in Figures 4 and 11 are real. On the other hand, Taylor & Wilson (1990) have argued that an amelioration of climate, and seemingly a divergence of pack ice cover, is involved with the penguin increase. Consistent with this idea is an increase in the size of latent-heat (wind-driven) polynyas during the past two decades in the RSShelfE (Parkinson 2002). Indeed, this penguin, as well as the whale, is very sensitive to sea-ice cover and polynya formation (Ainley 2002b, Ainley et al. 2003, Arrigo & van Dijken 2003). Now, however, it is difficult to choose between the relative roles of the whale removal experiment and climate influences. The Japanese fishery agency has been arguing that removing whales will provide more fish for human populations, and their experiment in the Ross Sea with respect to penguins may be demonstrating this point. Indeed, very provocative in this regard are the patterns of diatom production and grazing

described by Arrigo et al. (2002), although these authors did not consider the following explanation: in the western Ross Sea, populated during summer by a third of the World's Adélie penguins plus many foraging cetaceans — which together, presumably, are depleting their zooplankton grazing prey (see above) — diatoms are relatively ungrazed compared to the eastern Ross Sea where diatoms are heavily grazed, where most of the whale take has occurred and where the penguins are absent until the late summer. Thus, one explanation could be that the lower concentration of top predators has allowed a more robust concentration of zooplankton grazers to crop the diatoms.

Under CCAMLR, and because of Article XII, a huge and admirable effort is expended by a number of countries in what is called the CCAMLR Ecosystem Monitoring Program (CEMP; Constable et al. 2000). This program, however, is directed toward the low-latitude 'Antarctic marine ecosystem' and largely a fishery on Antarctic krill anticipated for more than two decades but which has yet to materialize. A rich literature predicts the ecosystem consequences of depleting krill, and on that basis the CEMP was developed (see Hutchison 2004). Although CEMP has yet to address it, fishing down the Antarctic toothfish stocks (and minke whales?) of high latitude neritic systems (RSShelfE) would have consequences as equally dramatic as fishing down the krill stocks of the 'Antarctic marine ecosystem.'

The RSShelfE is still at a point where it can be rescued intact and, with the emplacement of serious efforts to understand its food web dynamics, science can increase its positive contributions to the management of marine resources in the Antarctic and worldwide in the face of rapid climate change. This is now especially true, because species abundances and trophic processes at each marine trophic level can be determined far more quantitatively than could be achieved even in the recent past, with natural experiments (such as the extensive fast ice event discussed above) providing much further insight. New developments in marine science are available to quantify ecosystem processes like never before (see NSF 1998), but only recently has their use been introduced to the Antarctic. New, powerful assessment (e.g. Buckland et al. 1993, Clarke et al. 2003) and biochemical tracing techniques (e.g., Bottino 1974, Cripps & Hill 1998) can reveal trophic links and relationships, and exciting new technology, unavailable only a decade ago, can be used to precisely assess organism abundance simultaneously at multiple trophic levels, e.g. autonomous vehicles, BioMapper, and SeaSoar technology (e.g., Brierly et al. 2002). We may be amazed at what we learn about marine foodwebs upon applying this technology to other than the broken marine systems where it has been mostly perfected.

5.0 LITERATURE CITED

- AINLEY, D.G. 2002a. The Ross Sea, Antarctica: where all ecosystem processes still remain for study, but maybe not for long. *Marine Ornithology* 31: 55-62.
- AINLEY, D.G. 2002b. *The Adélie Penguin: Bellwether of Climate Change*. New York: Columbia University Press.
- AINLEY, D.G., C.A. RIBIC, G. BALLARD, S. HEATH, I. GAFFNEY, B.J. KARL, K.J. BARTON, P.R. WILSON & S. WEBB. 2003. Geographic structure of Adélie penguin

- populations: size, overlap and use of adjacent colony-specific foraging areas. *Ecological Monographs* 74: 159-178.
- AINLEY, D.G., C.T. TYNAN & I. STIRLING. 2003. Sea ice: a critical habitat for polar marine mammals and birds. In: D.N. Thomas & G.S. Diekman (Eds.) *Sea Ice: An Introduction to its Physics, Biology, Chemistry and Geology*. London: Blackwell Science, pp 240-266
- ANDERSON, P.J. & J.F. PIATT. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* 189: 117-123.
- ARRIGO K.R. & G.L. VAN DIJKEN. 2003. Phytoplankton dynamics within 37 Antarctic coastal polynya systems. *Journal of Geophysical Research*: 108 (C8), 3271, doi: 10.1029/2002JC002739.
- ARRIGO, K.R., D.L. WORTHEN & D.H. ROBINSON. 2003. A coupled ocean-ecosystem model of the Ross Sea: 2. Iron regulation of phytoplankton taxonomic variability and primary production. *Journal Of Geophysical Research* 108 (C7): 3231, doi:10.1029/2001JC000856
- ARRIGO, K.R., A.M. WEISS & W.O. SMITH JR. 1998. Physical forcing of phytoplankton dynamics in the western Ross Sea. *Journal of Geophysical Research* 103: 1007-1022.
- BARRY, J.P., J.M. GREBMEIER, J. SMITH & R. DUNBAR. 2003. Oceanographic versus bathymetric control of benthic megafaunal communities in the SW Ross Sea, Antarctica. In: G. DiTullio & R. Dunbar (Eds.) *Biogeochemistry of the Ross Sea. Antarctic Research Series* 78: 327-354.
- BATCHELDER, H., J.A. BARTH, P.M. KOSRO, P.T. STRUB, R.D. BRODEUR, W.T. PETERSON, C.T. TYNAN, M. D. OHMAN, L.W. BOTSFORD, T.M. POWELL, F.B. SCHWING, D.G. AINLEY, D.L. MACKAS, B.M. HICKEY & S.R. RAMP. 2002. The GLOBEC Northeast Pacific California Current Program. *Oceanography* 15: 36-47.
- BAUM, J.K., R.A. MYERS, D.G. KEHLER, B. WORM, S.J. HARLEY & P.A. DOHERTY. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science* 299: 389-392.
- BOTTINO, N.R. 1974. The fatty acids of Antarctic phytoplankton and euphausiids: fatty acid exchange among trophic levels of the Ross Sea. *Marine Biology* 27: 197-204.
- BRANCH, T.A. & D.S. BUTTERWORTH. 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.
- BRIERLY AS, PG FERNANDES, M.A. BRANDON, F. ARMSTRONG, N.W. MILLARD, S.D. MCPHAIL, P. STEVENSON, M PEBODY, J. PERRETT, M. SQUIRES, D.G. BONE & G. FRIFFITHS. 2002. Antarctic krill under sea ice: elevated abundance in a narrow band just south of the ice edge. *Science* 295:1890-1892.
- BROWN, M.R. & R.L BROWNELL. 2001. Review of catches of great whales taken in the proposed South Pacific sanctuary region. *International Whaling Commission SC 52/033*: 1-10.
- BROWN, J.H. & E.J. HESKE. 1990. Control of desert-grassland transition by a keystone rodent guild. *Science* 250: 1705-1708.
- BROWN, S.G. & C.H. LOCKYER. 1984. Whales. In: R.M. Laws (Ed.) *Antarctic Ecology*, Vol. 2. London: Academic Press, p717-781.
- BUCKLAND, S.T., D.R. ANDERSON, K.P. BURNHAM & J.L. LAAKE. 1993. *Distance Sampling*. London: Chapman & Hall.
- CALHAEM, I. & D.A. CHRISTOFFEL. 1969. Some observations of the feeding habits of a Weddell seal, and measurements of its prey, *Dissostichus mawsoni*, at McMurdo Sound, Antarctica. *New Zealand Journal of Marine and Freshwater Research* 3: 181-190.
- CARPENTER, S.R. & J.F. KITCHELL. 1988. Consumer control of lake productivity. *BioScience* 38: 764-769.

- CARPENTER, S.R., J.G. KITCHELL, J.R. HODGSON, P.A. COCHRAN, J.J. ELSER, D.M. LODGE, D. KRETCHMER, X. HE & C.N. VON ENDE. 1987. Regulation of lake primary productivity by food web structure. *Ecology* 68: 1863-1876.
- CCAMLR. 2002. The Ross Sea, Antarctica, where all ecosystem processes still remain for study. *CCAMLR Document No. WG-EMM-02/60*, Hobart, Tasmania.
- CLARKE, E.D., L.B. SPEAR, M.L. MCCRACKEN, F.F.C. MARQUES, D.L. BORCHERS, S.T. BUCKLAND & D.G. AINLEY. 2003. Validating the use of generalized additive models and at-sea surveys to estimate size and temporal trends of seabird populations. *Journal of Applied Ecology* 40: 278-292.
- CONSTABLE, A.J., W.K. DE LA MARE, D.J. AGNEW, I. EVERSON & D. MILLER. 2000. Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). *ICES Journal of Marine Science* 57: 778-791.
- CRIPPS, G.C. & H.J. HILL. 1998. Changes in lipid composition of copepods and *Euphausia superba* associated with diet and environmental conditions in the marginal ice zone, Bellingshausen Sea, Antarctica. *Deep-Sea Research I* 45: 1357-1381.
- DAYTON, P.D. 1985. The ecology of kelp communities. *Annual Review of Ecology and Systematics* 16: 215-245.
- DAYTON, P.K. 1990. Polar benthos. In: Smith, W.O. (Ed.) *Polar Oceanography*, Part B (Academic Press, New York. Pp. 631-686.
- DAYTON, P.K., B.J. MORDIDA & F. BACON. 1992. Polar marine communities. *American Zoologist* 34(1): 90-99.
- DEMASTER, D.J., R.B. DUNBAR, L.I. GORDON, A.R. LEVENTER, J.M. MORRISON, D.M. NELSON, C.A. NITTROUER & W.O. SMITH, JR. 1992. The cycling and accumulation of organic matter and biogenic silica in high-latitude environments: the Ross Sea. *Oceanography* 5: 146-153.
- DEVRIES, A.L. & J.T. EASTMAN. 1999. Brief review of the biology of *Dissostichus mawsoni*. *Proc CCAMLR*, Hobart, Tasmania. 5 pp.
- DITULLIO, G.R. & R.B. DUNBAR (Eds.). 2003. *Biogeochemistry of the Ross Sea*. Antarctic Research Series 78. Washington DC: American Geophysical Union.
- ELIANE, K., D.G. AKSNES, M.D. OHMAN, S. WOOD & M.B. MARTINUSSEN. 2002. Stage-specific mortality of *Calanus* spp. Under different predation regimes. *Limnology and Oceanography* 47: 636-645.
- 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., N.S. SMITH & J.F. PALMISANO. 1978. Sea otter predation and community organization in the western Aleutian Islands. *Ecology* 59: 822-833.
- ESTES, J.A., D.O. DUGGINS & G.B. RATHBUN. 1989. The ecology of extinctions in kelp forest communities. *Conservation Ecology* 3: 252-264.
- FRETWELL, S.D. 1987. Food chain dynamics: the central theory of ecology? *Oikos* 50: 291-301.
- HAIRSTON, N.G., JR. & N.G. HAIRSTON, SR. 1993. Cause-effect relationships in energy flow trophic structure and interspecific interactions. *American Naturalist* 142: 379-411.
- HEMPEL, G. 1985. Antarctic marine food webs. In: Siegfried, W.R., Condy, P.R. & Laws, R.M. (Eds) *Antarctic nutrient cycles and food webs*. Berlin: Springer Verlag. pp. 266-270.
- HORN, P.L. 2002. Age and growth of Patagonian toothfish (*Dissostichus eleginoides*) and Antarctic toothfish (*D. mawsoni*) in waters from the New Zealand subantarctic to the Ross Sea, Antarctica. *Fisheries Research* 56: 275-287.

- HUTCHISON, K. 2004. Fighting over fish. *Antarctic Sun*, 1 February 2004, pp 1, 16-19 (www.polar.org/antsun/index.htm).
- ICHII, T. & H. H. Kato. 1991. Food and daily food consumption of southern minke whales in the Antarctic. *Polar Biology* 11: 479-487.
- ICHII, T., N. SHINOHARA, Y. KUJISE, S. NISHIWAKI & K. MATSUOKA. 1998. Interannual changes in body fat condition index of minke whales in the Antarctic. *Marine Ecology Progress Series* 175: 1-12.
- JACKSON, J.B.C., M.X. KIRBY, W.H. BERGER, K.A. BJORN DAL, L.W. BOTSFORD, B.J. BOURQUE, R.H. BRADBURY, R. COOKE, J. ERLANDSON, J.A. ESTES, T.P. HUGHES, S. KIDWELL, C.B. LANGE, H.S. LENIHAN, J.M. PANDOLFI, C.H. PETERSON, R.S. STENEK, M.J. TEGNER & R.R. WARNER. Historical overfishing and the collapse of coastal ecosystems. *Science* 293: 629-637.
- KEUNNING, K. & K. HUTCHISON. 2003. Building a better base for science. *Antarctic Sun*, 16 November 2003, pp. 1, 9-10 (www.polar.org/sun).
- KIM, S., K. CONLAN, D. MALONE & C. LEWIS. Ms. Food hoarding in the Weddell seal: observations from McMurdo Sound, Antarctica. *Marine Mammal Science*, submitted (Feb 2004).
- KNOX, G.A. 1994. *The Biology of the Southern Ocean*. Cambridge: Cambridge University Press.
- LAWS, R.M. 1977. The significance of vertebrates in the Antarctic marine ecosystem. In: G.A. Llano (Ed.) *Adaptations within Antarctic ecosystems*. Washington DC: Smithsonian Institution, pp. 411-438.
- LEOPOLD, A. 1949. *A Sand County Almanac and Sketches Here and There*. New York: Oxford University Press (Special Commemorative Edition, 1989).
- MAY, R.M, J.R. BEDDINGTON, C.W. CLARKE, S.J. HOLT & R.M. LAWS. 1979. Management of multispecies fisheries. *Science* 205: 267-277.
- MCLAREN, B.E. & R.O. PETERSON. 1994. Wolves, moose, and tree rings on Isle Royale. *Science* 266: 1555-1558.
- MYERS, R.A. & B. WORM. 2003. Rapid worldwide decline of predatory fish communities. *Nature* 423: 280-283.
- NSF. 1998. *OEUVRE (Ocean Ecology: Understanding and Vision for Research)*. Workshop Report (www.joss.ucar.edu/joss_psg/project/oce_workshop/oeuvre/report).
- OHMAN, M.D., K. EIANE, E.G. DUBRIN, J.A. RUNGE & H.-J. HIRCHE. 2004. A comparative study of *Calanus finmarchicus* mortality patterns at five localities in the North Atlantic. *ICES Journal of Marine Science* 61: in press.
- OHSUMI, S. & Y. MASAKI. 1975. Biological parameters of the Antarctic minke whale at the virginal population level. *Journal of the Fisheries Research Board of Canada* 32: 995-1004.
- PACE, M.L., J.J. COLE, S.R. CARPENTER & J.F. KITCHELL. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* 14: 483-488.
- PARKINSON, C.L. 2002. Trends in the length of the Southern Ocean sea-ice season. *Annals of Glaciology* 34: 435-440.
- PAULY, D., V. CHRISTIANSEN, J. DALSGAARD, R. FROESER & F. TORRES JR. 1998. Fishing down marine food webs. *Science* 279: 860-863.
- PAULY, D. & J. MACLEAN. 2003. *In a Perfect Ocean: The State of Fisheries and Ecosystems in the North Atlantic Ocean*. Washington DC: Island Press.
- PITMAN R.L. & P. ENSOR. 2003. Three forms of killer whales in Antarctic waters. *Journal of Cetacean Research and Management* 5: 1-9.
- POST, D.M., M.E. CONNORS & D.S. GOLDBERG. 2000. Prey preference by a top predator and the stability of linked food chains. *Ecology* 81: 8-14.
- POWER, M.E. 1984. Depth distribution of armored catfish: predator-induced resource avoidance? *Ecology* 65: 523-528.

- POWER, M.E. 1990. Resource enhancement by indirect effects of grazers: armored catfish, algae, and sediment. *Ecology* 71: 897-904.
- POWER, M.E., W.J. MATTHEWS & A.J. STEWART. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of strong interaction. *Ecology* 65: 1448-1456.
- SHIOMOTO, A., K. TADOKORO, K. NAGASAWA & Y. ISHIDA. 1997. Trophic relations in the subarctic North Pacific ecosystem: possible feeding effect from pink salmon. *Marine Ecology Progress Series* 150: 75-85.
- SPRINGER, A.M., J.A. ESTES, G.B. VAN VLIET, T.M. WILLIAMS, D.F. DOAK, E.M. DANNER, K.A. FORNEY & B. PFISTER. 2003. Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences* 100: 12223-12228.
- STRONG, D.R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73: 747-754.
- TAYLOR, R.H. & P.R. WILSON. 1990. Recent increase and southern expansion of Adélie Penguin populations in the Ross Sea, Antarctica, related to climate warming. *New Zealand Journal of Ecology* 14: 25-29.
- TYNAN C.T. 2004. Cetacean populations on the Southeast Bering Sea shelf during the late 1990s: implications for decadal changes in ecosystem structure and carbon flow. *Marine Ecology Progress Series* 272: 281-300.
- TESTA, J.W., D.B. SINIFF, M.J. ROSS & J.D. WINTER. 1985. Weddell Seal - Antarctic Cod interactions in McMurdo Sound, Antarctica. In: Siegfried, W.R., P.R. Condy & R.M. Laws (Eds.) *Antarctic nutrient cycles and food webs* (Berlin: Springer Verlag. Pp. 561-565.
- VERITY, P.G. & V. SMETACEK. 1996. Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Marine Ecology Progress Series* 130: 277-293.
- WALTHER, G.-R., E. POST, P. CONVEY, A. MENZEL, C. PARMESAN, T.J.C. BEEBEE, J.-M. FROMENTIN, O. HOEGH-GULDBERG & F. BAIRLEIN. 2002. Ecological responses to recent climate change. *Nature* 416: 389-395.
- WILSON, P.R., D.G. AINLEY, N. NUR, S.S. JACOBS, K.J. BARTON, G. BALLARD & J.C. COMISO. 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.
- WOEHLER, E.J. 1995. Consumption of Southern Ocean marine resources by penguins. In: Dann, P., I. Norman & P. Reilly (Eds.) *The Penguins: Ecology and Management*. Chipping North, NSW: Surrey Beatty. Pp. 266-296.

7.0 ACKNOWLEDGEMENTS. This contribution was prepared by David Ainley. It benefited greatly from the comments of L. Blight, R. Brownell, P. Dayton, J. Estes, N. Gilbert, R. Hofman, S. Kim, S. Olmastroni, D. Siniff, P. Wilson, I. Stirling and C. Tynan.