



## Letter

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### Impacts of cetaceans on the structure of Southern Ocean food webs

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Recently, Ballance *et al.* (2006) revived the hypothesis that cetaceans were a major force in the structuring of Southern Ocean food webs, and suggested that they are still playing a keystone role even as their loss continues (see also review in Mori and Butterworth 2006), a subject that we herein would like to emphasize. According to this hypothesis, following 60 yr of directed industrial whaling (Tønnessen and Johnsen 1982, Baker and Clapham 2002), the demise of the great whales (blue, *Balaenoptera musculus intermedia*; fin, *B. physalus*; and humpback, *Megaptera novaeangliae*) led to changes in populations and demographic parameters among penguins, seals, and minke whales (*B. bonaerensis*; see also Laws 1977, Bengtson and Laws 1985). These changes to populations of the great whales' competitors came about upon release from trophic competition as a result of the "krill surplus" that ensued (*i.e.*, of Antarctic krill, *Euphausia superba*; Bengtson and Laws 1985).

Despite its popularity among Southern Ocean ecologists 25 yr ago, this top-down hypothesis (consumer effects on resources) has been largely replaced by an emphasis on bottom-up explanations (resource effects on consumers), as summarized in Ainley *et al.* (2007). Penguin populations and demographic parameters are still changing, but it is primarily geophysical causes that are now assigned as the drivers. Climate effects reducing sea ice with subsequent negative effects on krill abundance (*cf.* Fraser and Hofmann 2003, Atkinson *et al.* 2004), and in turn affecting predator trends, are the mechanisms most often invoked (*e.g.*, Forcada *et al.* 2006, Ducklow *et al.* 2007, Hinke *et al.* 2007). The longest time series on top trophic species are available for penguins and, indeed, elegant analyses have been conducted on penguin demographics in the Antarctic Peninsula and Adélie Land regions to support the links to climate change. This is clearly shown to be important in the northern Antarctic Peninsula region, but the same explanation has been used to explain negative penguin trends for waters off Adélie Land, East Antarctica, as well (see Barbraud and

Weimerskirch 2001, Jenouvrier *et al.* 2009), even though sea ice is expanding in that sector (Parkinson 2002, Zwally *et al.* 2002, Turner *et al.* 2009). Unfortunately, krill abundance has not been repeatedly measured there (*e.g.*, Nicol *et al.* 2000).

A challenge in attributing trends in populations of upper-trophic level predators to climate and ice-related krill declines alone is highlighted when the full complexity of the system is considered. For example, the humpback whale (*M. novaeangliae*), a trophic competitor of penguins (Friedlaender *et al.* 2008*a*; like penguins, they eat both krill and small fish: Laws 1977), has been increasing by 5% and an astounding 12%–13% per annum in waters off the Antarctic Peninsula and Adélie Land, respectively, with numbers going from near zero a few decades ago to many thousands in each region at present (Branch 2009). Blue whale (*B. musculus*) numbers are increasing as well in these areas, though far more slowly (Branch *et al.* 2007). Therefore, these whales have so far been finding sufficient food to sustain their population growth, apparently unlike Adélie (*Pygoscelis adeliae*) and other penguins of the Antarctic Peninsula and emperor penguins (*Aptenodytes forsteri*) of Adélie Land, or competing minke whales (Friedlaender *et al.* 2008*b*), whose populations have at least been stable though their body condition may be declining (*cf.* Branch 2006, Konishi *et al.* 2008). In the absence of further information, including whether whale foraging directly affects that of their competitors as noted elsewhere (*e.g.*, see Ainley *et al.* 2006*a*, Friedlaender *et al.* 2008*a, b*) or whether differences in ambits (space–time use patterns) are involved (whales, unlike penguins, are not tied to land colonies), an apparent paradox thus exists regarding decreasing krill availability and supposed effects on upper-level predators. Although they acknowledge that their modeling of upper-trophic-level predators is in its infancy, Mori and Butterworth (2006) concur that more than climate is involved in the explanation of large-scale changes in these species' populations in the Southern Ocean.

Here we present three ecological scenarios that demonstrate how cetaceans may influence the structure and dynamics of the Southern Ocean food web. These should be considered in addition to those suggested by Ballance *et al.* (2006, and references therein), Ainley *et al.* (2007), Willis (2007), and the seeming paradox described above. Marine trophic cascades resulting from top-predator removal are of course not a novel concept; examples in other ocean systems were recently summarized by Baum and Worm (2009). While we acknowledge the correlative nature of our examples, we nonetheless contend that these results indicate fruitful directions for current and future research in the Southern Ocean. Data from the Southern Ocean are most easily attained by remote sensing, which sheds light on why researchers are preoccupied with physical factors that lend themselves to this technology as ecosystem drivers (*e.g.*, Forcada *et al.* 2006, Ducklow *et al.* 2007, Hinke *et al.* 2007, Jenouvrier *et al.* 2009). While much of what we relate cannot be easily resolved using remote sensing, and instead requires direct observation, we hope our perspectives will enable the establishment of a broader scientific basis for management of Antarctic marine resources, which are increasingly coming under the pressure of cumulative impacts from climate change, fishing, and other anthropogenic factors (Blight and Ainley 2008).

KILLER WHALES (*ORCINUS ORCA*) AS PREDATORS OF LARGE PENGUINS

Barbraud and Cotté (2008) proposed that the International Whaling Commission (IWC) database on killer whale take and diet be consulted for evidence supporting our earlier hypothesis (Ainley *et al.* 2007) that a major removal of minke whales led to prey switching in killer whales, thus resulting in increased mortality of adult male emperor penguins during the late 1970s at Pointe Géologie, Adélie Land. We therefore examined the IWC database for the area within  $65^{\circ}$ – $66^{\circ}$ S,  $139^{\circ}$ – $141^{\circ}$ E (Pointe Géologie:  $66.8^{\circ}$ S,  $140.1^{\circ}$ E; Fig. 1). A large number of killer whales were taken by Russian whalers from this small area over 3 yr, 1978–1980 inclusive (Fig. 2), coincident with a return of adult emperor penguin survival rates to the approximately 20-yr mean (Fig. 2). None of this species was taken before, or after in that area.

None of the killer whales in the database was recorded as having penguin remains in their stomachs, but this absence is not definitive. Springer *et al.* (2008) pointed out the difficulty in gaining insights on diet from investigating killer whale stomach contents, given the common absence even of well-known prey items. Remains in killer whale stomachs provide useful information, but only constitute a dietary snapshot; the absence of penguin remains does not mean killer whales never eat penguins. For example, the IWC database also contains nine killer whales taken in the vicinity of Îles Crozet ( $46^{\circ}$ – $47^{\circ}$ S,  $50^{\circ}$ – $53^{\circ}$ E), where it is very well known that king penguins (*A. patagonicus*) are regularly eaten by killer whales (Guinet 1991, 1992). All nine of these whales lacked penguin remains in their stomachs. Like emperors, king penguins are large enough so that pursuing and catching them has an energetic reward for these large predators. In fact, no penguin remains are recorded in the database for any of the  $\sim 550$  killer whales taken south of  $44^{\circ}$ S since 1923 with identified stomach contents (81 more contained unidentifiable remains). Killer whales are also well known to regularly take king penguins at Marion Island ( $47^{\circ}$ S,  $38^{\circ}$ E; Condy *et al.* 1978), and at Macquarie Island,  $54^{\circ}$ S,  $159^{\circ}$ E; EW, personal observation). Marion Island is one location where the “cultural” aspects of predation have been studied, *i.e.*, many killer whale behaviors are found only in isolated family groups and passed down by teaching within the group (Tosh *et al.* 2008; see also Ford *et al.* 1998, for discussion of sociobiological aspects of killer whale diet elsewhere). The taking of penguins may be a cultural attribute that is not widespread among killer whales in general and would therefore be difficult to quantify from ocean-wide, undirected sampling, which is the basis of the IWC database (see below).

Also relevant here is the work of Williams *et al.* (2004), who showed how just a few killer whales can have a major impact on *K*-selected prey populations such as sea otters (*Enhydra lutris*). In terms of food value, an adult emperor penguin (body mass 22–24 kg at the end of chick rearing, twice that at the start of breeding; Williams 1995) would be energetically equivalent to a sea otter (23–34 kg) and approaching the energy density of a 40-kg Steller sea lion (*Eumetopias jubatus*) pup in the Williams *et al.*'s (2004) energetic modeling. Following the Williams *et al.* model, it would thus have required very few killer whales to have had significant impacts on the emperor penguin colony at Pointe Géologie. Pertinent, too, is the study by

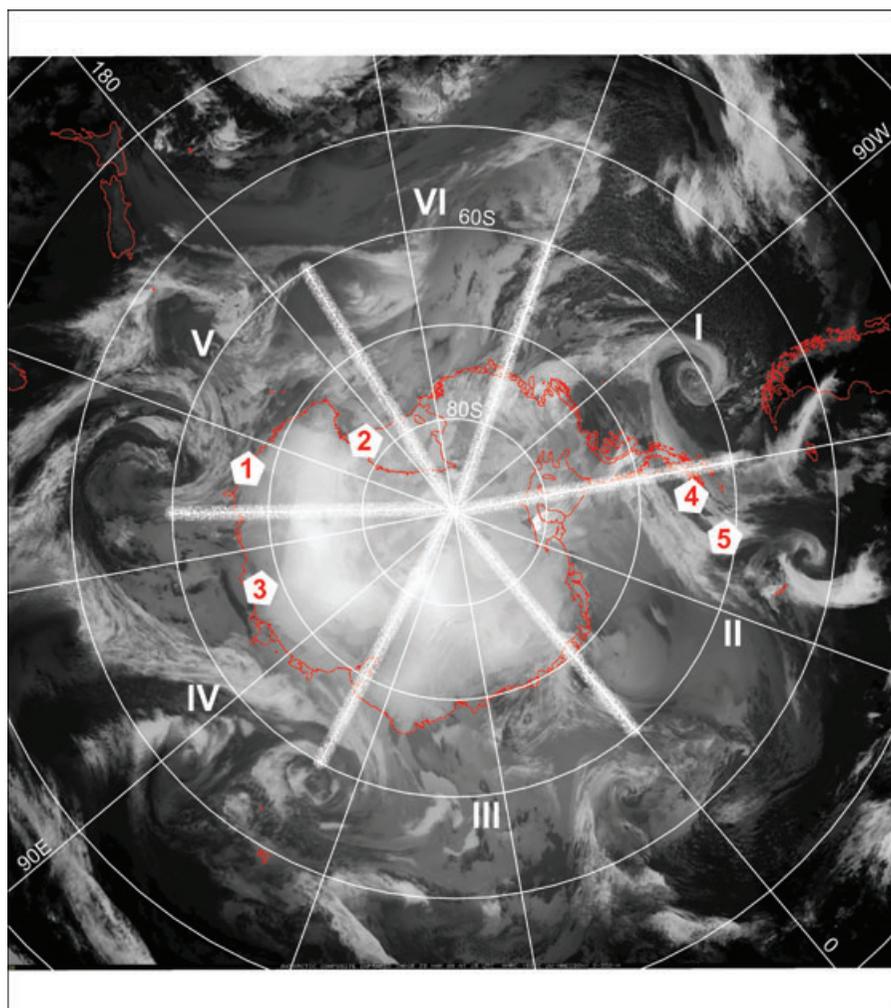
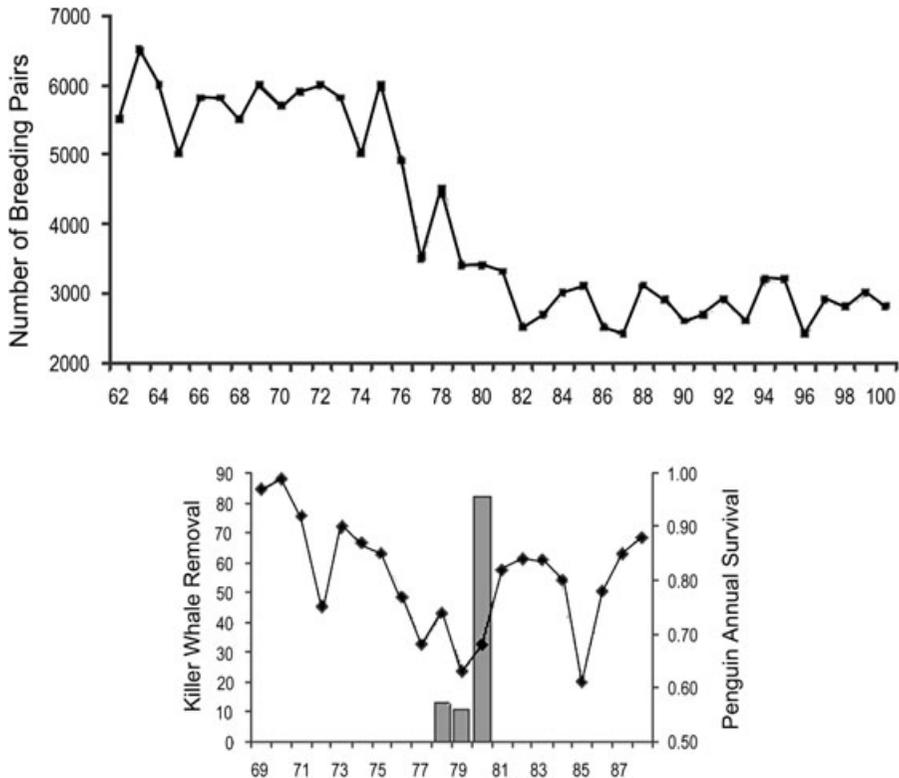


Figure 1. The Antarctic and Southern Ocean, showing locations mentioned in the text: IWC Areas I–VI, and the following by number: 1, Pointe Géologie; 2, Ross Island; 3, Law Dome; 4, James Ross Island; 5, Islas Orcadas (South Orkney Islands). Also shown are a series of storms of typical extent that move clockwise around the continent. Infrared satellite composite image (1500 UTC, 23 March 2009) made from a combination of geostationary and polar orbiting satellites (AMRC, SSEC, University of Wisconsin-Madison).

Boveng *et al.* (1998), who showed the extreme sensitivity of fur seal (*Arctocepalus gazella*) populations to predation by leopard seals (*Hydrurga leptonyx*), even when the predation is directed towards pups rather than the more demographically sensitive adults.

It is worthy to note that Andrews *et al.* (2008) attached a satellite tag to a type-B killer whale (see Pitman and Ensor 2003, for definition of ecotypes) in the vicinity of Cape Royds; the whale, and its pod, in an apparent “trap-line” sort of strategy, visited



*Figure 2.* Top, number of breeding pairs of emperor penguins at Pointe Géologie, 1965–2000. Bottom, annual survival of adult male emperor penguins at Pointe Géologie (line; data from Barbraud and Weimerskirch 2001), 1969–1988 (no data collected on survival before or thereafter), overlaying the number of potential predators, killer whales, removed from waters immediately off Pointe Géologie during a short time span (gray bars; from IWC database). Survival of adult penguins before 1969 and after 1988 was generally constant at the level indicated for these respective years, as the population did not vary during those times (see Barbraud and Weimerskirch 2001, Jenouvrier *et al.* 2009).

the sites of emperor penguin colonies as it moved north along the Victoria Land coast over subsequent weeks. Type-B killer whales have been observed patrolling one of these areas: the fast ice edge off the emperor penguin colony at Cape Washington (SO, personal observation), and have also been seen pursuing emperor penguins at Cape Royds (DGA and JP, personal observation). Lauriano *et al.* (2007) and Richlen and Thomas (2008; also PRW, personal observation) describe the behavior of killer whales in the western Ross Sea hunting Adélie penguins, although the extent of actual predation was uncertain (see also Visser *et al.* 2008, Ballard and Ainley 2005).

With these results in mind, the pattern presented in Figure 2 may indicate that the dramatic rebound in emperor penguin survival at Pointe Géologie was due to release from predation by the removal of an unprecedented  $\sim 100$  killer whales within 3 yr

from an area of just 185.2 km × 185.2 km immediately offshore from the colony. Modeling by Barbraud and Weimerskirch (2001) showed that much of the penguin decrease was due to an adult mortality “event.” The lack of population growth since has been related to reduced breeding success, corresponding to a “regime shift” in which increased winds and thinning ice has led to increased instability of the fast ice platform on which the penguins nest (*cf.* Ainley *et al.* 2005, Jenouvrier *et al.* 2005, Stammerjohn *et al.* 2008).

Such an “experiment,” *i.e.*, assessment of penguin demographic rates and colony trends upon removal of a major predator, was of course unintended, but it no doubt devastated the local killer whale population. Unfortunately, as is often a problem with “natural experiments,” results were confounded by other factors that could not be controlled—in this case by a coincident regime shift in meteorological conditions, as noted above. Other examples in which an upper-level predator population has coped with a regime shift, only to be reduced by an unrelated mortality event later, and from which it could not recover, have been reported for penguins and auks in the Galápagos Islands and coastal California, respectively (summarized in Ainley and Divoky 2001). We suggest that this removal experiment could also have extinguished or significantly reduced a “culture” (taking emperor penguins) among these killer whales. Explanation for the 1-yr return to low penguin survival 5 yr later (Fig. 2) is problematic, especially since data on numbers of killer whales in the vicinity do not exist for comparison with climate-related explanations (*cf.* Jenouvrier *et al.* 2009). The 60% reduction in the colony to just a couple of thousand pairs could have made it a less attractive food source for predators; only a portion of the population would be foraging at any given time. Nonetheless, a large dip in population size, which accompanied the increased mortality of the 1970s, had not been reported before nor since in this penguin population (Fig. 2).

Regardless of the observational evidence, the role of predation in emperor penguin demography remains a hypothesis to be further explored. Clearly, predation is unable to explain all of the variation in fluctuation of these penguins’ population, some of which is almost certainly related to climate-related processes, particularly with respect to breeding/foraging effort and chick productivity (Jenouvrier *et al.* 2009). Extent and thickness of fast ice and divergence of pack ice is likely involved (Ainley *et al.* 2005, Massom *et al.* 2009), including perhaps an indirect influence of increased risks (*i.e.*, foraging when predators are present) taken by starving male emperor penguins (*cf.* Alonzo 2002). These males fast for 4 mo during incubation, and likely hold an energetic debt until after the breeding process is completed (Williams 1995).

We look forward to continued recording and reporting of top-predator depredation events in the future (*e.g.*, Visser *et al.* 2008). That these are rarely reported is perhaps more indicative of the limited opportunities for observers to spend time at sea in high southern latitudes than it is to the absolute rarity of such events (see also Springer *et al.* 2008, who discussed the overall rarity with which killer whale predation events are observed).

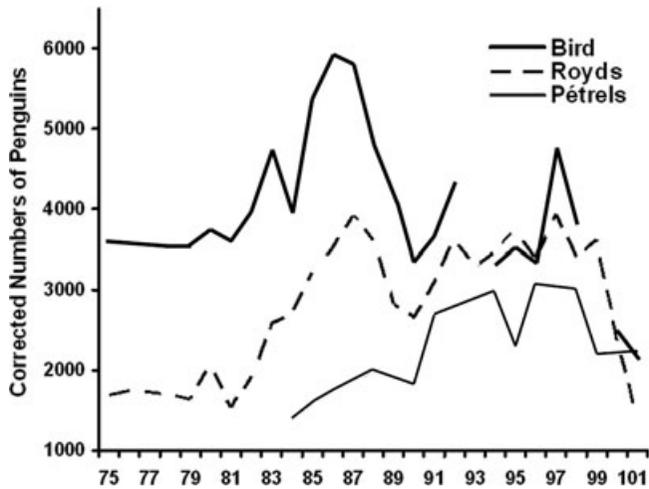


Figure 3. Annual variation in the number of Adélie penguins in the colony at Pétrels Island, Pointe Géologie, Adélie Land, 1984–2001, compared to that at two Ross Island colonies, Capes Royds and Bird, Victoria Land, by year 1975–2001. Data are from Wilson *et al.* (2001) and Jenouvrier *et al.* (2006), with numbers at Pétrels and Bird divided by 10 in order to be graphically comparable to those at the smaller Royds colony. The Pétrels data were used for Pointe Géologie as they did not show the effects, exhibited by other colonies in the area, of airfield construction at the Dumont d'Urville Station (see Jenouvrier *et al.* 2006 for details).

#### MINKE WHALES AS TROPHIC COMPETITORS OF PENGUINS

Barbraud and Cotté (2008) also suggested that if the reasoning of Ainley *et al.* (2007) is correct—that is, the removal of minke whales in IWC Area V led to an increase in food availability and subsequent competitive release of Adélie penguins in Victoria Land, eastern portion of Area V—then the same pattern should have occurred among penguins at Pointe Géologie, Adélie Land in the western portion of Area V (Fig. 1). Minke whales and Adélie penguins are direct trophic competitors (see Ainley *et al.* 2006a, b and references therein). The removal of 20,164 minke whales by commercial whaling in IWC Area V during ~15 yr in the 1970s and 1980s (see Brown and Brownell 2001) would not be ecologically trivial, particularly to penguins, even if this represents just 20% of the total minke population as noted by Barbraud and Cotté (2008). Even a small number of whales can have major impact on an area's food web structure and carbon flux (*e.g.*, Tynan 2004), and as whales are slow to reproduce, their population would not have rebounded quickly and thus the effects would have been long lived. In Area V, the majority of the minke whale take was in waters off George V Land coast and Terre Adélie, the region where many Victoria Land penguins spend their non-breeding period (G. Ballard *et al.*, unpublished data).

Inspection of penguin population change at colonies in East and West Area V do indeed show closely similar trends (Fig. 3); key is the point that an increase in the Pointe Géologie population was already underway when annual censuses began

in 1984. Indeed, Jenouvrier *et al.* (2006, p. 420) state that the “Adélie penguin population at Pointe Géologie Archipelago increased between 1984 and 2003 and showed similar fluctuations [to] Adélie populations on Ross Island [Victoria Land] between 1959 and 1997 . . . .” It is unfortunate that Adélie Land census data were not available earlier to compare with the earlier Ross Island data. Nonetheless, the comparison shows that it is plausible to conclude that whatever was influencing population trends of Victoria Land Adélie penguins was also affecting those of Adélie Land (Pointe Géologie). Whether all this translates to a mechanism driving regional penguin population trends is certainly speculative, but is consistent with the earlier tenets of the “krill surplus” resulting from whale removal, and past explanations of changes in whale-penguin-seal populations elsewhere (Ballance *et al.* 2006). We conclude here by suggesting that both bottom-up and top-down factors have been involved in interrelated ways in this scenario (see Ainley *et al.* 2005, 2007; Jenouvrier *et al.* 2006).

#### WHALES, KRILL, AND THE METHANESULFONIC ACID RECORD OF EAST ANTARCTIC ICE CORES

Whales may figure in another much-researched phenomenon as well, with their removal perhaps contributing to a region-wide shift and trophic cascade involving the plankton and nekton communities. Recently, Ainley *et al.* (2007) hypothesized that the decrease of krill in the Southwest Atlantic sector (SWAS, or IWC Area II and western Area III; Fig. 1) beginning in the 1970s (Atkinson *et al.* 2004) was a possible factor behind a decrease in methanesulfonic acid (MSA) detected in glacial ice cores during the same period (Curran *et al.* 2003). MSA is one of the two (with sulfur dioxide) major end products of dimethylsulfide (DMS), which itself originates from dimethylsulfoniopropionate (DMSP) produced by phytoplankton. When krill graze on phytoplankton (especially diatoms) and break down their cell walls, DMSP is released into seawater, whereas grazing by pelagic salps (*Salpa thompsoni*) does not release DMSP as the salps do not destroy the cell walls during ingestion (Kasamatsu *et al.* 2004). Salp prevalence has been increasing in the SWAS since the 1970s, replacing krill (Atkinson *et al.* 2004); thus, this replacement might affect atmospheric levels of MSA.

Curran *et al.* (2003) detected a change in MSA deposition in glacial cores and attributed this solely to a reduction in sea ice during the 1950s–1960s in Areas II and III. Eschewing any biologically driven processes, it has been suggested that the krill–phytoplankton association with the marginal ice zone is involved (Kawaguchi *et al.* 2005, but see Atkinson *et al.* (2008), who argue for equally high krill abundance away from ice edges). Alternate explanations for the MSA decrease seem necessary, however, as Curran *et al.* (2003) pointed out that the correlation between pack ice extent and prevalence of MSA in glacial ice cores from East Antarctica was not valid everywhere around Antarctica (Röthlisberger and Abram 2009), nor even globally (O’Dwyer *et al.* 2000). Moreover, well-considered papers in physical oceanography have questioned whether any large-scale sea ice reduction would have been possible in this region during the 1950s–1960s (*cf.* Murphy *et al.* 1995; De La Mare 1997,

2008; *vs.* Ackley *et al.* 2003; Jacobs 2006). The most conclusive results come from Jacobs (2006), who found no evidence for changes in surface salinity in the Southern Ocean hydrographic record during the period in question. This is the only direct record that overlaps the entire period 1950s to the present, other than the ice core record itself. Such a salinity change would have to have happened if any large-scale reduction occurred in sea ice extent, a result indirectly confirmed by Cotté and Guinet (2007) who noted that any ice decrease would have been local and short term. Surface salinity, along with temperature, is one of the most conservative, easily-determined and long-standing measures of water mass characteristics.

In the context of this background, what factors were behind the change in MSA in the East Antarctic ice cores? Ultimately, as noted by Curran *et al.* (2003), the exclusive source of MSA in ice cores is marine phytoplankton (*e.g.*, see also Yoch 2002). Importantly, their glacial ice core site, Law Dome (66°S, 110°E; Fig. 1), projects far into the Southern Ocean, is greatly influenced by marine air from the prevailing westerly winds and has substantial annual snow accumulation rates. Therefore, the MSA in the Law Dome cores must be from the ocean to the west, *i.e.*, the SWAS. As salps have been replacing krill in the region (above), the atmospheric availability of DMS/MSA to Law Dome should be decreasing (see Ainley *et al.* 2007). Despite the distances involved, movement of air-borne compounds from the SWAS to Law Dome is easily tenable considering the eastward movement of fronts and storms in the region (Fig. 1)—South American dust blown southeastward is found in ice cores obtained from the Antarctic Peninsula (McConnell *et al.* 2007, Fig. 1), and dust from Asia blown eastward is a major component in the analysis of ice cores of Greenland (see Alley 2000, Mayewski and White 2002).

Indeed, the MSA record presented in Curran *et al.* (2003) shows a long period of increase beginning ~1910 and peaking in the 1950s (Fig. 4). This trend corresponds closely with the cumulative take of krill foraging, long-lived baleen whales during the Antarctic industrial whaling era, most of which was in Areas II and III (*cf.* Tønnessen and Johnsen 1982, Tynan 1998; Fig. 1). The effect would have been cumulative because the great whales are slow to reproduce and normally live on the order of 100 yr or longer. Storminess, *i.e.*, the frequency and intensity of storms moving eastward from Area I to III (Fig. 1), would also affect the amount of MSA available for incorporation into snow, and ultimately glacial ice, on the continent, as noted by Curran *et al.* (2003, supplementary material). Controlling for this (two-way linear regression) and using the amount of South American dust in Antarctic Peninsula ice cores as a storminess index (McConnell *et al.* 2007), a highly statistically significant relationship is shown between MSA and cumulative barrels of oil (a proxy for whale loss and the krill surplus;  $r^2 = 0.59$ ,  $P < 0.001$ ; Fig. 5). This model accounts for upward bulges in MSA that occurred in 1920–1927 and again 1936–1946 (Fig. 4), with elevated dust concentrations occurring in ice cores indicating increased storminess in the region during those periods. Therefore, the MSA record may well be a strong proxy for ecosystem effects of the removal of whales and the purported krill surplus (see, again, Ballance *et al.* 2006). This trophic cascade involving multiple trophic levels is worth further investigation as such.

Sub-peaks of MSA in the mid-1800s (see Curran *et al.* 2003) are consistent as well with the hypothesis of Emslie and Patterson (2007) that an apparent major dietary shift from fish to krill in Adélie penguins began at that time, which was when millions of krill-eating fur seals were hunted to near extinction in the SWAS. The penguins apparently switched to the growing superabundance of Antarctic krill (Emslie and Patterson 2007). We hypothesize, therefore, that vastly increased abundance of krill in the SWAS led to increased release of DMS/MSA from the mid-1800s to the 1960s. Thereafter, MSA prevalence in the ice cores decreased, consistent with (see fig. 1 in Ainley *et al.* 2007): (1) eventually reduced krill production in response to grazing by whales (Willis 2007); (2) the rise of salps—replacing krill—owing to release from predation due to extensive depletion of their fish predators (especially nototheniids) beginning in the 1960s, and concurrent climate factors (Loeb *et al.* 1997, Ainley and Blight 2009); and (3) the increasing effects in recent decades of climate and sea ice forces bearing directly and negatively on krill abundance, as discussed by Atkinson *et al.* (2004).

If further analyses of the Curran *et al.* (2003) findings indicate that MSA concentration in ice cores is a proxy, at least in part, for the relative abundance of Antarctic krill (and their grazing) in the SWAS, rather than being due just to the amount of sea ice cover and storminess, it would be a paradigm-changing discovery. East Antarctic

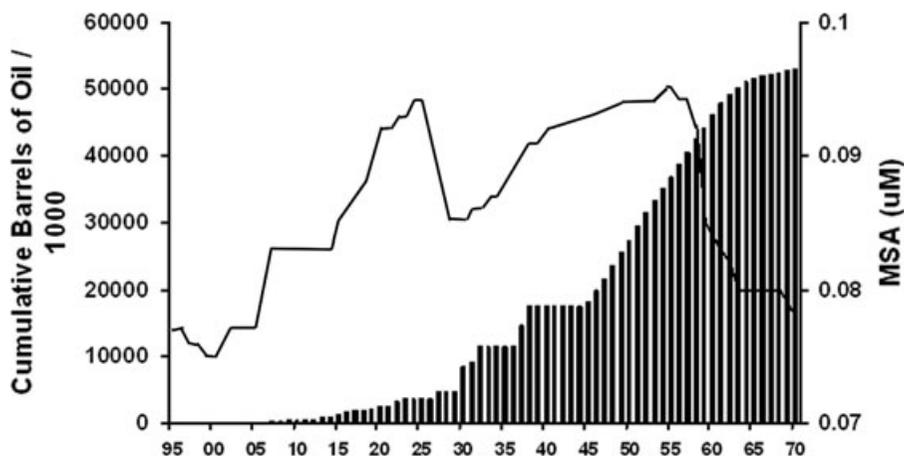


Figure 4. The cumulative barrels of whale oil taken from the Antarctic (bars; data from Tønnessen and Johnsen 1982), as a proxy for the extraction of krill-grazing whales and thus an increase in the abundance of krill foraging on diatoms (the “krill surplus”), compared to the MSA record in the Law Dome ice core (solid line; from Curran *et al.* 2003), by year 1895–1970. Given that the whales taken would normally live on the order of 100 yr, the effect of removal would be cumulative for the period of study. Tønnessen and Johnsen (1982) acknowledged incomplete records, which account for some of the plateaus and other patterns in the figure (*e.g.*, no whaling during WWII); these authors also indicated that Antarctic whale populations were already being depleted in the 1890s by whaling on wintering grounds at lower latitudes. See Ainley *et al.* (2007, fig. 1) for a closer look at the period after the late 1950s, when climate factors may have begun to affect krill abundance and in turn MSA availability.

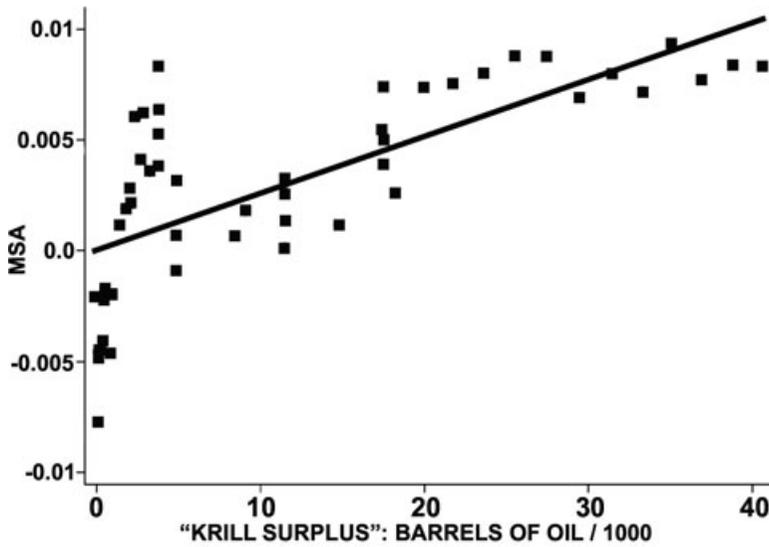


Figure 5. The relationship between storminess-corrected MSA ( $\mu\text{M}$ , *i.e.*, the residual in a regression for MSA concentration on storminess), with MSA data from Law Dome (#3 in Fig. 1; data from Curran *et al.* 2003), as indexed by the amount of South American dust in Antarctic Peninsula ice cores (James Ross Island, #4; and Islas Orcadas, #5 in Fig. 1; data from J. McConnell), *vs.* the krill surplus, as indexed by the cumulative barrels of whale oil taken 1905–1957 ( $r^2 = 0.59$ ,  $P < 0.001$ ; data from Tønnessen and Johnsen 1982) mostly from IWC Areas II and III (as shown in Tynan 1998).

ice cores could then be used to track relative changes in the prehistoric, historic, and future abundance of Antarctic krill in the SWAS and perhaps elsewhere in the Southern Ocean.

#### CONCLUDING THOUGHTS

The above three sections present a suite of hypotheses on the direct role of top-down pressures involving cetaceans in structuring Southern Ocean food webs. Recent population fluctuations of cetaceans, as top predators, appear to play an important role in past and present changes seen in the Antarctic marine ecosystem (see also Mori and Butterworth 2006). Incorporating ecological processes of trophic cascades, competition, predation, and facilitation into models attempting to address climate effects on populations should result in a more realistic understanding of these systems. Indeed, owing to simplification via the loss of top-most predators and the ongoing removal of other predators (large fish), much of the Southern Ocean ecosystem is currently in a potentially fragile state, further compromising its ability to withstand rapid climate change (see Österblom *et al.* 2007, Cury *et al.* 2008, Watermeyer *et al.* 2008a, b).

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#### LITERATURE CITED

- Ackley, S., P. Wadhams, J. C. Comiso and A. P. Worby. 2003. Decadal decrease of Antarctic sea ice extent inferred from whaling records revisited on the basis of historical and modern sea ice records. *Polar Research* 22:19–25.
- Ainley, D. G., and L. K. Blight. 2009. Ecological repercussions of historical fish extraction from the Southern Ocean. *Fish and Fisheries* 10:13–38.
- Ainley, D. G., and G. J. Divoky. 2001. Seabirds: Effects of climate change. Pages 2669–2677 in J. Steele, S. Thorpe, and K. Turekian, eds. *Encyclopedia of ocean sciences*. Academic Press, London, U.K.
- Ainley, D. G., E. D. Clarke, K. Arrigo, W. R. Fraser, A. Kato, K. J. Barton and P. R. Wilson. 2005. Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean, 1950s to the 1990s. *Antarctic Science* 17:171–182.
- Ainley, D. G., G. Ballard and K. M. Dugger. 2006a. Competition among penguins and cetaceans reveals trophic cascades in the Ross Sea, Antarctica. *Ecology* 87:2080–2093.
- Ainley, D., V. Toniolo, G. Ballard, K. Barton, J. Eastman, B. Karl, S. Focardi, G. Kooyman, P. Lyver, S. Olmastroni, B. Stewart, J. W. Testa and P. Wilson. 2006b. Managing ecosystem uncertainty: Critical Habitat and dietary overlap of top-predators in the Ross Sea. CCAMLR document EMM 06–07, Hobart, Tasmania, Australia.
- Ainley, D. G., G. Ballard, S. Ackley, L. K. Blight, J. T. Eastman, S. D. Emslie, A. Lescroël, S. Olmastroni, S. E. Townsend, C. T. Tynan, P. Wilson and E. Woehler. 2007. Paradigm lost, or, is top-down forcing no longer significant in the Antarctic marine ecosystem? *Antarctic Science* 19:283–290.
- Alley, R. 2000. *The two-mile time machine*. Princeton University Press, Princeton, NJ.
- Alonzo, S. H. 2002. State-dependent habitat selection games between predators and prey: The importance of behavioural interactions and expected lifetime reproductive success. *Evolutionary Ecology Research* 4:759–778.
- Andrews, R. D., R. L. Pitman and L. T. Ballance. 2008. Satellite tracking reveals distinct movement patterns for Type B and Type C killer whales in the southern Ross Sea, Antarctica. *Polar Biology* 31:1461–1468.
- Atkinson, A., V. Siegel, E. Pakhomov and P. Rothery. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432:100–103.
- Atkinson, A., V. Siegel, E. A. Pakhomov, P. Rothery, V. Loeb, R. M. Ross, L. B. Quetin, K. Schmidt, P. Fretwell, E. J. Murphy, G. A. Tarling and A. H. Fleming. 2008. Oceanic circumpolar habitats of Antarctic krill. *Marine Ecology Progress Series* 362:1–23.
- Baker, C. S., and P. J. Clapham. 2002. Marine mammal exploitation: Whales and whaling. Volume 3. Causes and consequences of global environmental change. Pages 446–450 in I. Douglas and T. Munn, eds. *Encyclopedia of global environmental change*. John Wiley and Sons, Ltd., Chichester, UK.

- Ballance, L., R. L. Pitman, R. P. Hewitt, D. B. Siniff, W. Z. Trivelpiece, P. J. Clapham and R. L. Brownell, Jr. 2006. The removal of large whales from the Southern Ocean: Evidence for long-term ecosystem effects? Pages 215–230 in J. A. Estes, D. P. Demaster, D. F. Doak, T. E. Williams and R. L. Brownell, Jr., eds. Whales, whaling and ocean ecosystems. University of California Press, Berkeley, CA.
- Ballard, G., and D. G. Ainley. 2005. Killer whale harassment of Adélie penguins at Ross Island. *Antarctic Science* 17:385–386.
- Baum, J. K., and B. Worm. 2009. Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, doi: 10.1111/j.1365-2656.2009.01531.x.
- Barbraud, C., and C. Cotté. 2008. Paradigms need hypothesis testing: No evidence for top-down forcing on Adélie and emperor penguin populations. *Antarctic Science* 20:391–392.
- Barbraud, C., and H. Weimerskirch. 2001. Emperor penguins and climate change. *Nature* 411:183–186.
- Bengtson, J. L., and R. M. Laws. 1985. Trends in crabeater seal age at maturity: An insight into Antarctic marine interactions. Pages 669–975 in W. R. Siegfried, P. R. Condy and R. M. Laws, eds. Antarctic nutrient cycles and food webs. Springer-Verlag, Berlin, Germany.
- Blight, L. K., and D. G. Ainley. 2008. Southern Ocean not so pristine. *Science* 321:1443.
- Boveng, P. L., L. M. Hiruki, M. K. Schwartz and J. L. Bengtson. 1998. Population growth of Antarctic fur seals: Limitation by a top predator, the leopard seal? *Ecology* 79:2863–2877.
- Branch, T. A. 2006. Abundance estimates for Antarctic minke whales from three completed circumpolar sets of surveys, 1978/79 to 2003/04. Paper SC/58/IA18, International Whaling Commission, Cambridge, U.K.
- Branch, T. A. 2009. Humpback abundance south of 60S from three completed sets of IDCR/SOWER circumpolar surveys. *Journal of Cetacean Research and Management*. In press.
- Branch, T. A., K. M. Stafford, D. M. Palacios, C. Allison, J. L. Bannister, C. L. K. Burton, E. Cabrera, C. A. Carlson, B. Galletti Vernazzani, P. C. Gill, R. Hucke-Gaete, K. C. S. Jenner, M.-N. M. Jenner, K. Matsuoka, Y. A. Mikhalev, T. Miyashita, M. G. Morrice, S. Nishiwaki, V. J. Sturrock, D. Tormosov, R. C. Anderson, A. N. Baker, P. B. Best, P. Borsa, R. L. Brownell, Jr., S. Childerhouse, K. P. Findlay, T. Gerrodette, A. D. Ilangakoon, M. Joergensen, B. Kahn, D. K. Ljungblad, B. Maughan, R. D. McCauley, S. McKay, T. F. Norris, Oman Whale and Dolphin Research Group, S. Rankin, F. Samaran, D. Thiele, K. Van Waerebeek and R. M. Warneke. 2007. Past and present distribution, densities and movements of blue whales *Balaenoptera musculus* in the Southern Hemisphere and northern Indian Ocean. *Mammal Review* 37:116–175.
- Brown, M. R., and R. L. Brownell, Jr. 2001. Review of catches of great whales taken from the proposed South Pacific Sanctuary region. Report SC52/O33, International Whaling Commission, Cambridge, U.K.
- Condy, P. R., R. J. Van Aarde and M. N. Bester. 1978. The seasonal occurrence and behaviour of killer whales *Orcinus orca* at Marion Island. *Journal of Zoology London* 184:449–464.
- Cotté, C., and C. Guinet. 2007. Historical whaling records reveal major regional retreat of Antarctic sea ice. *Deep-Sea Research I* 54:243–252.
- Curran, M. A. J., T. D. Van Ommen, V. I. Morgan, K. L. Phillips and A. S. Palmer. 2003. Ice core evidence for sea ice decline since the 1950s. *Science* 302:1203–1206.
- Cury, P. M., Y.-J. Shin, B. Planque, J. M. Durant, J.-M. Fromentin, S. Kramer-Schadt, N. C. Stenseth, M. Travers and V. Grimm. 2008. Ecosystem oceanography for global change in fisheries. *Trends in Ecology and Evolution* 23:338–346.
- De La Mare, W. K. 1997. Abrupt mid-twentieth-century decline in Antarctic sea ice extent from whaling records. *Nature* 389:57–60.
- De La Mare, W. K. 2008. Changes in Antarctic sea-ice extent from direct historical observations and whaling records. *Climatic Change* 92:461–493.

- Ducklow, H. W., K. Baker, D. G. Martinson, L. B. Quetin, R. M. Ross, R. C. Smith, S. E. Stammerjohn, M. Vernet and W. Fraser. 2007. Marine pelagic ecosystems: The West Antarctic Peninsula. *Philosophical Transactions of the Royal Society of London Series B* 362:67–94.
- Emslie, S. D., and W. P. Patterson. 2007. Abrupt recent shift in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in Adélie penguin eggshell in Antarctica. *Proceedings of the National Academy of Sciences* 104:1666–1669.
- Forcada, J., P. N. Trathan, K. Reid, E. J. Murphy and J. P. Croxall. 2006. Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biology* 12:411–423.
- Ford, J. K. B., G. M. Ellis, L. G. Barrett-Lennard, A. B. Morton, R. S. Palm and K. C. Balcomb III. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology* 76:1456–1471.
- Fraser, W. R., and E. E. Hofmann. 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Marine Ecology Progress Series* 265:1–15.
- Friedlaender, A. S., W. R. Fraser, D. Patterson, S. S. Qian and P. N. Halpin. 2008a. The effects of prey demography on humpback whale (*Megaptera novaeangliae*) abundance around Anvers Island, Antarctica. *Polar Biology* 31:1217–1224.
- Friedlaender, A. S., G. L. Lawson and P. N. Halpin. 2008b. Evidence of resource partitioning between humpback and minke whales around the western Antarctic Peninsula. *Marine Mammal Science* 25:401–415.
- Guinet, C. 1991. Intentional stranding apprenticeship and social play in killer whales (*Orcinus orca*). *Canadian Journal of Zoology* 69:2712–2716.
- Guinet, C. 1992. Comportement de chasse des orques (*Orcinus orca*) autour des îles Crozet. *Canadian Journal of Zoology* 70:1656–1667.
- Hinke, J. T., K. Salwicka, S. G. Trivelpiece, G. M. Watters and W. Z. Trivelpiece. 2007. Divergent responses of *Pygoscelis* penguins reveal a common environmental driver. *Oecologia* 153:845–855.
- Jacobs, S. 2006. Observations of change in the Southern Ocean. *Philosophical Transactions of the Royal Society Series A* 364:1657–1681.
- Jenouvrier, S., C. Barbraud and H. Weimerskirch. 2006. Sea ice affects the population dynamics of Adélie penguins in Terre Adélie. *Polar Biology* 29:413–423.
- Jenouvrier, S., H. Caswell, C. Barbraud, M. Holland, J. Strøve and H. Weimerskirch. 2009. Demographic models and IPCC climate projections predict the decline of an emperor penguin population. *Proceedings of the National Academy of Sciences* 106:1844–1847.
- Jenouvrier, S., H. Weimerskirch, C. Barbraud, Y.-H. Park and B. Cazelles. 2005. Evidence of a shift in the cyclicity of Antarctic seabird dynamics linked to climate. *Proceedings of the Royal Society B* 272:887–895.
- Kasamatsu, N., S. Kawaguchi, S. Watanabe, T. Odate and M. Fukuchi. 2004. Possible impacts of zooplankton grazing on dimethylsulfide production in the Antarctic Ocean. *Canadian Journal of Fisheries and Aquatic Sciences* 61:736–743.
- Kawaguchi, S., N. Kasamatsu, S. Watanabe, T. Odate, M. Fukuchi and S. Nicol. 2005. Sea ice changes inferred from methanesulphonic acid (MSA) variation in East Antarctic ice cores: Are krill responsible? *Antarctic Science* 17:211–212.
- Konishi, K., T. Tamura, R. Zenitani, T. Bando, H. Kato and L. Walløe. 2008. Decline in energy storage in the Antarctic minke whale (*Balaenoptera bonaerensis*) in the Southern Ocean. *Polar Biology* 31:1509–1520.
- Lauriano, G., C. M. Fortuna and M. Vacchi. 2007. Observation of killer whale (*Orcinus orca*) possibly eating penguins in Terra Nova Bay, Antarctica. *Antarctic Science* 19:95–96.
- Laws, R. M. 1977. Seals and whales of the Southern Ocean. *Philosophical Transactions of the Royal Society of London Series B* 279:81–96.

- Loeb, V., V. Siegel, O. Holm-Hansen, R. Hewitt, W. Fraser, W. Trivelpiece and S. Trivelpiece. 1997. Effects of sea-ice extent on krill or salp dominance on the Antarctic food web. *Nature* 387:897–900.
- Massom, R. A., K. Hill, C. Barbraud, N. Adams, A. Ancel, L. Emmerson and M. J. Pook. 2009. Fast ice distribution in Adélie Land, East Antarctica: Interannual variability and implications for emperor penguins *Aptenodytes forsteri*. *Marine Ecology Progress Series* 374:243–257.
- Mayewski, P. A., and F. White. 2002. *The ice chronicles, the quest to understand global climate change*. University Press, Lebanon, NH.
- McConnell, J. R., A. J. Aristarain, J. R. Banta, P. R. Edwards and J. C. Simões. 2007. 20th-Century doubling in dust archived in an Antarctic Peninsula ice core parallels climate change and desertification in South America. *Proceedings of the National Academy of Sciences* 104:5743–5748.
- Mori, M., and D. S. Butterworth. 2006. A first step towards modelling the krill–predator dynamics of the Antarctic ecosystem. *CCAMLR Science* 13:217–277.
- Murphy, E. J., A. Clarke, C. Symon and J. Priddle. 1995. Temporal variation in Antarctic sea-ice: Analysis of a long term fast-ice record from the South Orkney Islands. *Deep-Sea Research I* 42:1045–1062.
- Nicol, S., T. Pauly, N. L. Bindoff, S. Wright, D. Thiele, G. W. Hosie, P. G. Strutton and E. Woehler. 2000. Ocean circulation off east Antarctica affects ecosystem structure and sea-ice extent. *Nature* 406:504–507.
- O'Dwyer, J., E. Isaksson, T. Vinje, T. Jauhainen, J. Moore, V. Pohjola, R. Vaikmäe and R. S. W. van de Wal. 2000. Methanesulfonic acid in a Svalbard ice core as an indicator of ocean climate. *Geophysical Research Letters* 27:1159–1162.
- Österblom, H., S. Hansson, U. Larsson, O. Hjerne, F. Wulff, R. Elmgren and C. Folke. 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. *Ecosystems* 10:877–889.
- Parkinson, C. L. 2002. Trends in the length of the Southern Ocean sea ice season, 1979–99. *Annals of Glaciology* 34:435–440.
- Pitman, R. L., and P. Ensor, P. 2003. Three forms of killer whales (*Orcinus orca*) in Antarctic waters. *Journal of Cetacean Research and Management* 5:1–9.
- Richlen M. F., and J. A. Thomas. 2008. Acoustic behavior of Antarctic killer whales (*Orcinus orca*) recorded near the ice edge of McMurdo Sound, Antarctica. *Aquatic Mammals* 34:448–457.
- Röthlisberger, R., and N. Abram. 2009. Sea-ice proxies in Antarctic ice cores. *PAGES News* 17:24–26. Available at: [http://www.pages-igbp.org/products/newsletters/ref2009\\_1.html](http://www.pages-igbp.org/products/newsletters/ref2009_1.html).
- Stammerjohn, S. E., D. G. Martinson, R. C. Smith, X. Yuan and D. Rind. 2008. Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño–southern oscillation and southern annular mode variability. *Journal of Geophysical Research* 113, C03S90, doi:10.1029/2007JC004269.
- Springer, A. M., J. A. Estes, G. B. Van Vliet, T. M. Williams, D. F. Doak, E. M. Danner and B. Pfister. 2008. Mammal-eating killer whales, industrial whaling, and the sequential megafaunal collapse in the North Pacific Ocean: A reply to critics of Springer et al. 2003. *Marine Mammal Science* 24:414–442.
- Tønnessen, J. N., and A. O. Johnsen. 1982. *The history of modern whaling*. C. Hurst, London, U.K.
- Tosh, C. A., P. J. Nico De Bruyn and M. N. Bester. 2008. Preliminary analysis of the social structure of killer whales, *Orcinus orca*, at subantarctic Marion Island. *Marine Mammal Science* 24:929–940.
- Turner, J., J. C. Comiso, G. J. Marshall, T. A. Lachlan-Cope, T. Bracegirdle, T. Maksym, M. P. Meredith, Z. Wang and A. Orr. 2009. Non-annular atmospheric circulation change induced by stratospheric ozone depletion and its role in the recent increase of Antarctic sea ice extent. *Geophysical Research Letters* 36, L08502, doi:10.1029/2009GL037524.
- Tynan, C. T. 1998. Ecological importance of the southern boundary of the Antarctic Circumpolar Current. *Nature* 392:708–710.

- Tynan, C. T. 2004. Cetacean populations on the southeastern Bering Sea shelf during the late 1990s: Implications for decadal changes in ecosystem structure and carbon flow. *Marine Ecology Progress Series* 272:281–300.
- Visser, I. N., T. G. Smith, I. D. Bullock, G. D. Green, O. G. L. Carlsson and S. Imberti. 2008. Antarctic Peninsula killer whales (*Orcinus orca*) hunt seals and a penguin on floating ice. *Marine Mammal Science* 24:225–234.
- Watermeyer, K. E., L. J. Shannon, J.-P. Roux and C. L. Griffiths. 2008a. Changes in the trophic structure of the southern Benguela before and after the onset of industrial fishing. *African Journal of Marine Science* 30:351–382.
- Watermeyer, K. E., L. J. Shannon, J.-P. Roux and C. L. Griffiths. 2008b. Changes in the trophic structure of the northern Benguela before and after the onset of industrial fishing. *African Journal of Marine Science* 30:383–403.
- Williams, T. D. 1995. *The penguins*. Oxford University Press, Oxford, U.K.
- Williams, T. M., J. A. Estes, D. G. Doak and A. M. Springer. 2004. Killer appetites: Assessing the role of predators in ecological communities. *Ecology* 85:3373–3384.
- Willis, J. 2007. Could whales have maintained a high abundance of krill? *Evolutionary Ecology Research* 9:1–12.
- Wilson, P. R., D. G. Ainley, N. Nur, S. S. Jacobs, K. J. Barton, G. Ballard and 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.
- Yoch, D. C. 2002. Dimethylsulfoniopropionate: Its sources, role in the marine food web, and biological degradation to dimethylsulfide. *Applied and Environmental Microbiology* 68:5804–5815.
- Zwally, H. J., J. C. Comiso, C. L. Parkinson, D. J. Cavalieri and P. Gloersen. 2002. Variability of Antarctic sea ice 1979–1998. *Journal of Geophysical Research* 107, doi:10.1029/2000JC000733.

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