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Opinion

Projecting the effects of environmental change on Antarctic seals

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Abstract: We consider how Antarctic seals may respond to changes in climate, realizing that anthropogenic alteration of food webs will influence these responses. The species considered include the ice-obligate - crabeater (*Lobodon carcinophaga*), Weddell (*Leptonychotes weddellii*), Ross (*Ommataphoca rossii*) and leopard (*Hydrurga leptonyx*) seal - and the ice-tolerant Antarctic fur seal (*Arctocephalus gazella*) and southern elephant seal (*Mirounga leonina*). The data analysed are from long-term censuses of Weddell seals in McMurdo Sound (1997–2006), and of Weddell, fur and elephant seals at Arthur Harbour, Antarctic Peninsula (1974–2005). After considering their responses to recent changes in environmental features, as well as projected and current changes to their habitat our conclusions are that the distribution and abundance of 1) crabeater and Weddell seals will be negatively affected by changes in the extent, persistence and type of annual sea ice, 2) Ross and leopard seal will be the least negatively influenced by changes in pack ice characteristics, although, as may be the case for crabeater and Weddell, population size and distribution may be altered through changes in food web dynamics, and 3) southern elephant and fur seals will respond in ways opposite to the pack ice species, but could also be influenced most immediately by changes in their food resources due to factors other than climate.

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Introduction

It is well documented that the earth's atmosphere, on average, is warming, causing regional adjustments in temperatures, winds and precipitation, and that these effects are amplified in polar regions (IPCC 2007). The latter changes have much to do with sea ice and its reflective properties in a positive feedback loop: higher temperature, less ice, less reflection of the sun's energy, more heat absorption by the increasing area of dark ocean, etc. (e.g. Russell *et al.* 2006). While changing climate is affecting vertebrate species directly or indirectly in many parts of the world, the changing sea ice regime is likely to have direct effects on 'pagophilic' species, such as polar bears (*Ursus maritimus* Phipps) in the Arctic (Stirling & Parkinson 2006) and, as we argue here, pinnipeds in the Antarctic. The four species of pack ice seals (crabeater, *Lobodon carcinophagus* (Hombron & Jacquinot), Weddell, *Leptonychotes weddellii* Lesson, Ross, *Ommatophoca rossii* (Gray), and leopard, *Hydruga leptonyx* (Blainville)) rely on sea ice for most or at least critical portions of their life-history and demonstrate particular sensitivity to even small changes in the sea ice physical and biological environment (see summaries in Erickson *et al.* 1971, Gilbert & Erickson 1977, Bester & Hofmeyr 2007). On the other hand, two species are ice tolerant (Antarctic fur seal, *Arctocephalus gazella* (Peters 1875) and related spp., and southern elephant seal, *Mirounga leonina* L.), in that they occasionally occur in the vicinity of sea ice and may haulout onto its surfaces, but, although elephant seals have been reported to breed on ice (Laws 1956), reproduction is usually dependent on the availability of land. Elsewhere, other members of these genera are successful in the total absence of ice. In light of potential changes in the environment of these species, we consider the importance of life-history patterns as the basis for predicting which of these species will be most affected initially, and what we might expect if climate continues to change as projected by the IPCC. Our effort here is similar to that of Croxall *et al.* (2002) who explored the consequences of climate change on three Antarctic seabird species. It is possible that the pack ice seals are more sensitive to changes in sea ice patterns than are seabirds (with the exception of the emperor penguin, *Aptenodytes* *forsteri* Gray) as these seals depend on sea ice for critical parts of their reproductive activities.

We develop our argument by describing responses of pinnipeds to ice conditions using existing observations and by creating a sensitivity index (Laidre *et al.* in press), the results of which provide our collective assessment of how the different seal species probably will be influenced by physical and biological changes as climate change proceeds. We first consider the changes in the environment relevant to Antarctic seal species that have been well documented. Then we discuss changes that are likely in the near future, and suggest how these have been and will be interacting with the known life-history traits of the six seal species. The predictions made here regarding seal responses to environmental change are based on the fact that these species have evolved traits that are highly dependent, at least at the large scale, on a very stable, predictable physical environment (Ingolfsson *et al.* 1998, Smith *et al.* 1999). The annual cycle of pack ice development, though quite variable seasonally and inter-annually, has been extremely predictable at a longer time scale with respect to important physical features such as ice development, persistence, and extent. The Antarctic seal species have evolved traits that depend on this larger-scale predictability.

Methods

Recent environmental changes

Changes in sea ice extent and persistence during the past few decades have been recorded by satellite remote sensing. Zwally *et al.* (2002) and Parkinson (2002) have considered the trends in sea ice for all the major sectors of the Southern Ocean (see also Jacobs 2006). Major contrasting, but complementary, changes have been occurring in the Ross Sea and Bellingshausen regions during the most recent three decades, in large part mediated by the Southern Annular Mode (Jacobs 2006, Stammerjohn *et al.* 2008). That is, sea ice extent has been increasing in the Ross Sea but decreasing in the Antarctic Peninsula sectors. Further, the sea ice season in the Ross Sea region has been lengthening, but coastal polynyas within the larger-scale ice field all around the continent have been expanding (Parkinson 2002). These changes during late autumn to early spring, influence the length of time it takes sea ice to recede during summer. Thus, in regions where the persistence and extent of winter ice has declined (Bellingshausen and southern Scotia seas), spring-summer ice has become much reduced over major areas. Where sea ice has expanded in persistence, the ice edge is also further away from the continent and takes more time to recede to summer locations (see also Jacobs & Giulivi 1998, Bester & Odendaal 2000, Stammerjohn *et al.* 2008). In recent years the summer sea ice in the northern Bellingshausen and Antarctic Peninsula regions has been virtually absent (Fig 1a; Ducklow *et al.* 2007). Off East Antarctica it has changed little, but in the Ross Sea sector, except for coastal polynyas, the sea ice field in spring is larger and more concentrated, leaving less space between ice floes. As a result, it recedes more slowly during summer. In addition, high latitude McMurdo Sound has recently experienced a short-term 'natural experiment' of markedly changed sea ice invoked by the grounding of major icebergs that have broken from the nearby Ross Ice Shelf (Arrigo *et al.* 2002). This event instantly altered the seasonal sea ice patterns and growing polynya (see below).

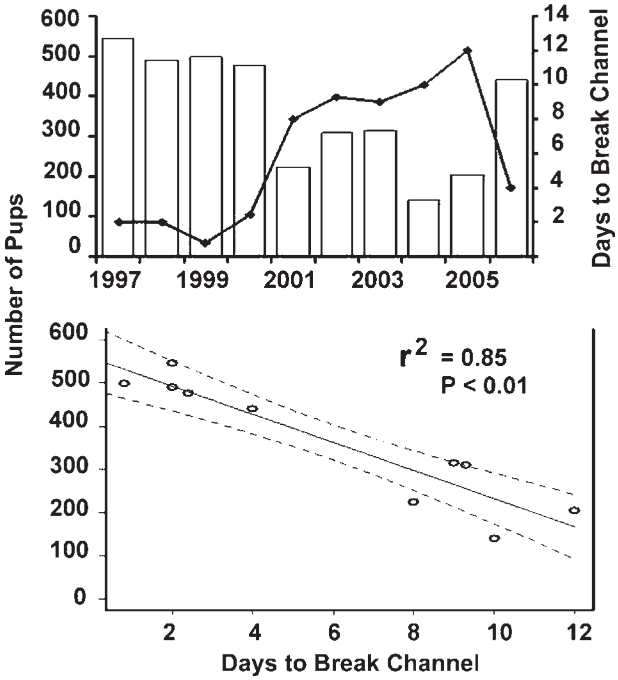

Fig. 1. Top, the number of pups born to Weddell seals in southern McMurdo Sound, an index to the number of females present, 1997–2006, and the number of days required to break the ice channel to McMurdo Station (dark line). Bottom, the relationship between ice thickness (as depicted by the number of days to open the ship channel to McMurdo Station) and number of pups born into the population ($r = -0.93$, $P < 0.01$).

Developing a sensitivity index

To summarize and compare our conjectures on the probable response of seals to habitat change, we used the type of sensitivity index developed for Arctic marine mammals by Laidre *et al.* (in press). Our version of the index focuses mostly on sea ice and the subsequent consequences of its changes to the ecosystem and its food webs using six factors that, depending on region, are currently responding to climate change: 1) sea ice persistence, 2) sea ice extent, 3) ice floe size and structure, 4) ice shelf breakage, 5) changes in food resources, and 6) changes in accessible beach areas. We also included a seventh category representing food web changes related to industrial fishing.

Each factor was scored between +4 and -4. Negative changes were inferred to be detrimental and positive ones beneficial to a given life history. Ranking was initially calculated by each author, with the agreed-upon final rating a consensus finding. In the paragraphs that follow, we provide the logic used to reach a final consensus regarding the influence of environmental change on each seal species' population and distribution. Obviously, this exercise only serves to illustrate and summarize the relative importance of environmental changes and the final tallies of scores cannot be taken just at face value. A case in point is the fur seal, which probably is mostly benefiting from a warming Antarctic Ocean (ocean south of the Polar Front; less ice, positive scores), but would be hard hit by industrial fishing (negative scores). Thus its final score comes to zero, which points to its situation being more complex than for the other species and not that it will be unaffected by environmental change.

Ice definitions

Fast ice is sea ice locked in place late into the summer by capes, islands or grounded ice bergs. *Sea ice extent* (SIE) refers to the large-scale spread of ice, usually viewed from the coast to its northernmost edge, at maximum in late winter 100s if not 1000s of kilometres away from the coast. *Sea ice concentration* refers to the proportion of the region that is covered by ice relative to open water (leads, polynyas); ice concentration at the large scale co-varies with SIE (Jacobs & Comiso 1989, Zwally *et al.* 2002). *Ice area* is the amount of ice in a region, minus any leads or polynyas between ice floes, i.e. minus any open water. *Ice thickness* refers to the measurement between the air-ice and the water-ice boundaries of ice. Finally, a *polynya* is an area within the pack ice that is ice free or of significantly reduced ice concentration relative to the surrounding ice. Polynya size in the Ross Sea Polynya, as an example, co-varies directly with large scale sea ice extent, as both are wind generated (Jacobs & Comiso 1989). Pack ice is sea ice broken into ice pieces (floes) from metres to kilometres in area, with water (leads) between the floes.

Results

Pack ice seal life histories

In this section of the paper we examine the general life-history characteristics of the four species of pack ice seals concentrating on those traits that are likely to become maladaptive as a result of changing sea ice attributes.

Crabeater seal

The crabeater is the most abundant seal species in the world (Laws 1977). It has evolved to be a specialist in its foraging habits and feeds almost exclusively on Antarctic krill (*Euphausia superba* Dana) in pelagic and slope areas, and crystal krill (*E. crystallorophias* Holt & Tattersall) in neritic areas. So important have krill become to its diet that its dentition has evolved to filter krill from sea water. The mating and pupping season begins in October and probably continues to early November, with the exact timing varying by region (Southwell *et al.* 2003). During this period females occupy ice floes that are selected for their size and physical characteristics (Siniff *et al.* 1979). Here, a female gives birth to a pup and is soon joined by a male, who is apparently waiting for the pup to be weaned and the female to enter oestrus and become available for mating. The ice floe occupied must be large enough that it does not break up until the pup is weaned in about 4–6 weeks. Also, the selected floes usually have some structure that the female uses to advantage in order to thwart the advances of the male who constantly attempts to separate her from the pup (forced weaning), thus, to advance the onset of oestrus. The surface relief may also provide a visual shield against both leopard seals and killer whales (*Orcinus orca* (L.)), which are major predators (Siniff & Bengtson 1977). Killer whales have been known to create waves that displace seals from floes (Smith *et al.* 1981, Pitman & Ensor 2003, Visser *et al.* 2008). Of the four species of pack ice seals, the crabeater may be the most vulnerable to predation. Leopard seals focus particularly on pups, and killer whales are a constant threat to all age classes. In nearly every region of the Antarctic Ocean, a significant proportion (60–70%) of crabeater seals show scars that indicate escape from a leopard seal (Siniff & Stone 1985). Thus, the structure and size of ice floes are very important to protect this species from predation.

Any environmental changes that will affect the availability of Antarctic krill will probably have an impact on crabeater seals (see similar comments for certain seabirds in Croxall *et al.* 2002). It is well known that Antarctic krill are highly dependent on sea ice, particularly during winter, when juvenile krill feed on under-ice microbial organisms and escape predation; as sea ice disappears so has the local abundance of Antarctic krill (Fraser & Hofmann 2003, Atkinson *et al.* 2005). On the other hand, on more restricted continental shelf areas, more persistent and growing coastal polynyas should lead to increased prevalence of crystal krill (see Pakhomov & Perissinotto 1996).

Areas where sea ice has and will continue to exhibit the above changes should exhibit a decline in crabeater abundance due to direct (pupping platform and protection from predators) and indirect (food supply) influences. On the other hand, as some changes may initially increase the availability of crystal krill, regional contradictions in population trends could become evident.

Leopard seal

The leopard seal has a diverse diet and is a major predator on many vertebrate species in the sea ice regions (Laws 1977).

Table I. A matrix summarizing how environmental change may influence life-history patterns and, ultimately, the population dynamics of Southern Ocean seals. Arbitrary values between ± 4 were chosen to show the predicted degree of effect. Positive values indicate improved conditions because of climate change, while negative values indicate detrimental effects. "Food web changes" relate only to the effect of climate change on the pack ice ecosystem and ultimately krill availability.

	Sea ice persistence	Sea ice extent and concentration	Floe size and structure	Ice shelf losses	Breeding beach availability	Food web changes	Industrial fishing	Net effects
Pack ice seals								
Crabeater	-4	-4	-3	0	0	-4	-4	-19
Leopard	-1	-3	-1	0	-1	-2	-2	-10
Weddell	-4	-2	-3	0	-1	-1	-4	-15
Ross	-1	-2	-3	0	0	-1	-2	-9
Ice tolerant species								
Elephant seal	1	1	0	2	3	0	-4	3
Fur seal	1	1	0	2	3	-3	-4	0

Its diet choice varies seasonally and spatially, with krill sometimes dominating during winter, switching to crabeater seal pups during spring, and focusing on fledgling penguins as they go to sea in late summer. Fish are also a common prey item and can be taken throughout the annual cycle. The leopard seal is known to visit islands in the lower latitudes, and sometimes remains there throughout the year. Many of these are juveniles and often in poor condition. Whether more adults would join this trend as climate change proceeds is unknown, but such behaviour modification should be considered (Bester *et al.* 2006). In spite of this general trophic pattern (Siniff & Stone 1985), some individuals become specialists and remain in one region, concentrating on a particularly vulnerable prey such as penguins (Kooyman 1965). Such behaviour has been documented also in the case of predation on fur seal (*A. gazella*) pups (Hiruki *et al.* 1999).

The pupping season occurs in spring, but few observations have been made of pups with females (Siniff & Stone 1985, Southwell *et al.* 2003). Based on appearance, it is hypothesized that the pup can enter the water fairly early in the lactation period and may accompany the female as she forages. Breeding may not follow weaning immediately, as is the case with the other pack ice species, but may be postponed, perhaps as much as a month after weaning has occurred (Siniff & Stone 1985). However, the exact timing of oestrus and breeding needs further data.

Leopard seals are known to use many different types and sizes of ice floes for resting, pupping and moulting. They are seen on bits of ice bergs as well. They are preyed upon by killer whales (see Ainley *et al.* 2005a), so larger, more protective ice floes are probably selected if available. Satellite telemetry shows that individuals may stay within one general area for extended periods (Rogers *et al.* 2005).

In considering the four factors concerned with ice in our sensitivity matrix, we predict that changes in any of them will not have a large influence on this species. Sea ice persistence and floe size and structure would seem to have little effect because of the ability of this species to use many different ice floe types and move location if ice floe availability becomes limited. Because of their diverse diet, food shortages may not be a problem and thus we have lowered the degree of negative impact (Table I). However, we offer a caveat to this assessment as there is a lack of information on the diet of juveniles, and juvenile survival may be a critical life-history stage.

Weddell seal

This species spends much of its time close to the Antarctic continent, where colonies form in early spring along predictable cracks in the persistent fast ice. In late winter and early spring, prior to pupping, these seals spend much of their time under this fast ice and use their teeth to keep breathing holes open where the ice is thin near perennial tide cracks. At high latitudes, e.g. McMurdo Sound (78°S), females haulout in late October and early November to give birth; at lower latitudes, e.g. the South Orkneys (60°S), pupping is in September (Testa *et al.* 1990). The pups are weaned 6–7 weeks after birth, and copulation occurs under the ice. As the fast ice begins to deteriorate, adults and newly-weaned pups disperse. Satellite tracking of McMurdo Sound animals shows that some individuals move north into the Ross Sea (Burns *et al.* 1999, Ainley *et al.* 2006). Weddell seals are known to feed principally on Antarctic silver fish (*Pleuragramma antarcticum* Boulenger), the Antarctic toothfish (*Dissostichus mawsoni* Norman) and several species of cephalopods (Burns *et al.* 1998, La Mesa *et al.* 2004, Kim *et al.* 2005, Ainley *et al.* 2006, Ponganis & Stockard 2007).

In McMurdo Sound, where all pups born to this population have been marked since the 1970s and annual estimates of adults present have been made, relationships to several ice-related factors that affect population trends, behaviour and physiology have become obvious (Cameron & Siniff 2004). Testa *et al.* (1991), linking climatological patterns to the dynamics of this population, found a relationship to El Niño–Southern Oscillation (ENSO), probably mediated through changes in ice extent and concentration (lower extent during ENSO; see Ledley 1997, Jacobs & Giulivi

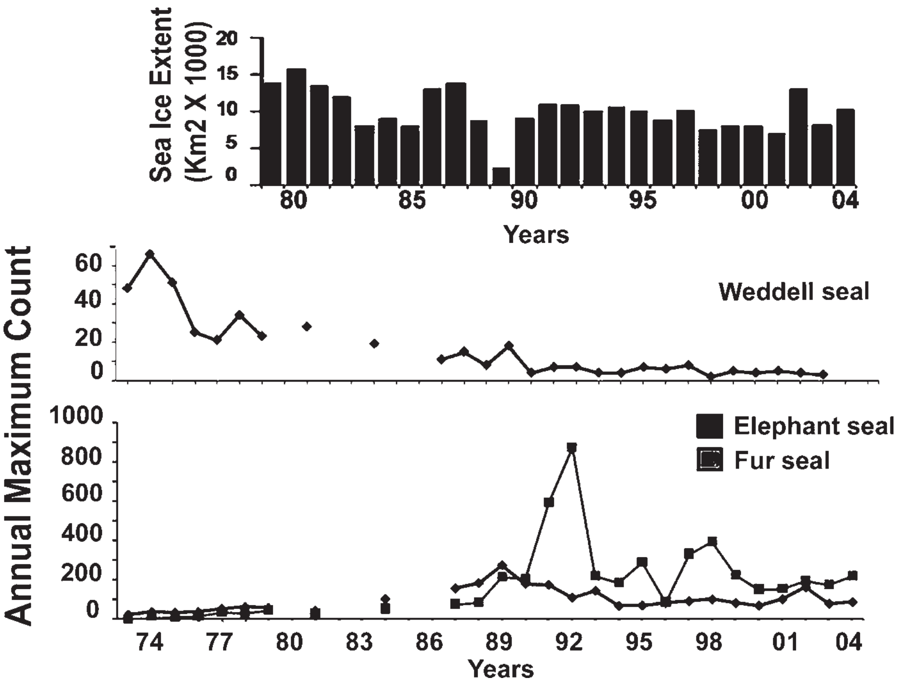

Fig. 2. Ice area in the "Long Term Ecological Research (LTER) study area," west coast of Antarctic Peninsula, 1979–2004, as determined by satellite imagery (Spearman correlation, ice vs year: r = -0.43; p = 0.03; data from Ducklow *et al.* 2007). The maximum number of pinnipeds of three species counted among all censuses in a given year on the islands within that study area: Arthur Harbour, Anvers Island, 1974–2005 (see text for statistical relationship between ice and seal numbers).

1998). More recently, elaborating on this relationship and with a longer time series, Hadley *et al.* (2007a) reported that pup incidence among females tended to be lower when sea ice was more extensive in the previous year's post-weaning period and hypothesized that more sea ice in that period would lead to decreased foraging success for pregnant females. Possibly the decreased foraging success with more pack ice is related to the reduced amount of open water available for phytoplankton blooms and primary productivity (Arrigo & van Dijken 2004), which ultimately should affect fish availability. In support of this explanation, Proffitt *et al.* (2007) demonstrated that foraging success of pregnant Weddell seals (reflected by the weaning mass of their eventual pups) decreased during summers characterized by extensive sea ice. Further, Hadley (2006) found modest evidence that years of extensive winter sea ice were followed by years of higher survival among adult females. This is in accord with the increased productivity hypothesis, in that winters of extensive ice (which tend also to have more concentrated ice) are followed by summers of minimal ice (Jacobs & Comiso 1989). Finally, Hadley *et al.* (2007b) reported that females were more likely to give birth to their first pup during a spring following a winter with more sea ice in the Ross Sea region, i.e. a winter often following a summer of minimal ice.

For Weddell seals, insight into the possible demographic consequences of long-term fluctuations in fast ice persistence was provided when a large portion of the Ross Ice Shelf broke off in late 2000. The resulting iceberg blocked the usual advection of sea ice from McMurdo Sound until winter 2006. As a result, the fast ice increased in extent, thickness, and seasonal persistence. This is indicated by the relative difficulty for an icebreaker to make a channel to McMurdo Station (Fig. 1a). Weddell seals were directly affected, presumably from the increased ice thickness, which in some cases closed off cracks that had been predictably present in previous years. As a result, fewer adults showed up for breeding and fewer pups were born (Fig. 1b). It is unknown whether McMurdo Sound females pupped elsewhere. This could certainly be the case, but, if so, based on normally high philopatry, it seems likely that pupping elsewhere would result in higher pup mortality. Over a 10-year period a strong negative relationship existed between the proxy of ice thickness and the number of pups born (r = -0.93, $P < 0.01$; Fig 1b). However, it is interesting to note how quickly the number of pups born to this population returned to previous levels when the effect of the iceberg was removed. This suggests that the seals were in the vicinity but, in the situation of reduced productivity owing to regionally more extensive, concentrated, and persistent pack ice (Arrigo & van Dijken 2004), were "choosing" not to breed. No doubt other species in the fast ice ecosystem, which have evolved to take advantage of the stable conditions that exist in fast-ice areas, were also affected (e.g. Dayton 1989).

In contrast, in the Antarctic Peninsula region over the past few decades, sea ice has diminished in extent, concentration, and especially persistence (Zwally *et al.* 2002, Parkinson 2002, Stammerjohn *et al.* 2008; Fig. 2a). Weekly counts of seals instituted in 1974 from various shore locations in Arthur Harbour (vicinity of Palmer Station) show that the number of Weddell seals has gradually declined (Fig. 2b; seals vs year, $r_s = -0.896$, $P < 0.001$). We do not know the exact reason for the decline but presume it has to do with the reduction in the region of the amount of fast ice necessary for breeding (Fig. 1a, ice extent, $r_s = 0.457$, $p = 0.07$). The general picture that emerges for Weddell seals with respect to the sensitivity matrix suggests that this species will be influenced either by increasing thickness of near-shore ice, or change in prevalence or persistence of fast ice areas. That is, any environmental event that holds potential to alter what historically have been seasonally predictable fast ice areas will greatly influence this species through the pupping and breeding seasons and thus we scored the maximum effect for sea ice persistence (Table I). We predict that both sea ice extent and ice floe size and structure would have less effect upon this species. In this case we felt that floe size and structure would be most important for protection from killer whale predation. In neritic areas, larger polynyas could mean enhanced productivity and availability of prey, mediated through crystal krill.

Ross seal

This species is much less abundant than the other pack ice seals. It is highly pelagic, seldom seen, and large concentrations have never been noted. Few pups have been sighted, but the occasional records suggest pupping occurs on ice floes in spring, with exact timing dependent on the region of the Antarctic (Thomas *et al.* 1980, Southwell *et al.* 2003). Like the other species, the pupping season probably varies with location. During a cruise into the Amundsen Sea sector during late 1999 and early 2000 (Ackley *et al.* 2003), Ross seals were found moulting on very large ice floes, often a kilometre across (Siniff, personal observation). Their appearance at this time was of sloughing skin similar to elephant seals. These large floes may be very critical at this time, as the seals may be at a disadvantage energetically if forced to enter the water. In regard to diet, analyses indicate that Ross seals feed predominantly on cephalopods. Recent satellite tracking indicates that this species may move north and beyond 60°S, and remain in ice-free waters for some time (Blix & Nordoy 2007).

With respect to our sensitivity matrix, only ice floe size during pupping and moulting is probably important to this species, and we have ranked this factor the most detrimental. Sea ice concentration co-varies with ice floe size and thus we considered this factor next most important (Table I). The effects of changes in sea ice on Ross seal foraging seems unlikely to be detrimental since they often forage at considerable distances from the continent, beyond the sea ice, and thus may be preying on species not particularly tied to the pack ice ecosystem.

Ice tolerant seal life histories

Southern elephant seals and sub-Antarctic (*A. tropicalis* Gray) and Antarctic (*A. gazella*) fur seals were hunted during the 1700–1800s, exterminating some island populations completely and bringing others to near extinction (Matthews 1977, Croxall 1992). Since then, both have returned to virtually all former sub-Antarctic and low latitude Antarctic breeding colonies, with some populations fully recovered by the 1970s (Laws 1977, Croxall 1992, Weimerskirch *et al.* 2003). At some locations, as at South Georgia, fur seals are beginning to crowd out other species (e.g. Bonner 1985). However, in recent decades, beginning in the 1970s, elephant seals have been declining, including populations at Macquarie, Heard, Marion, Kerguelen and Crozet islands (Weimerskirch *et al.* 2003, McMahon & Burton 2005); at South Georgia, where half the world population breeds, they've been stable, and at Valdés, Argentina, in temperate waters (outside of the Southern Ocean), they have been increasing (McMahon & Burton 2005). At South Georgia their population stability is probably related to a limited amount of available breeding space (Boyd 1993). Both species have been increasing further south, e.g. at Anvers Island (Fig. 2b). In regard to feeding, the two species differ markedly. Like the Weddell seal, the elephant seal is a deep diver, capable of reaching several hundred metres (Jonker & Bester 1994); the fur seal, like the crabeater and leopard seal, feeds within 200 m of the surface (Robinson *et al.* 2002).

Southern elephant seal

This species breeds on beaches, including pebble, cobble and boulder beaches, as well as on vegetated areas behind landing beaches, and exceptionally on ice (e.g. Laws 1956, Condy 1978a). As the females come ashore, groups coalesce, sometimes with several hundred on one beach. Meanwhile, males compete for supremacy to insure access to females. One "beachmaster" might control 40–50 females depending on structure of the beach. Females give birth to pups within a few days after arriving. They enter oestrus about 19 days after giving birth and are receptive for breeding for about four days. They often copulate with the dominant male of the area, although low ranking males may also participate in the breeding. Females remain with the pup until weaning (23 days after being born), which usually occurs in about 30 days after hauling out. At this time females leave the beach to feed and recover weight lost during lactation, after which they return to moult. Males return to moult later than females; younger animals return to moult before the adults (Condy 1979, Kirkman *et al.* 2003a, 2004). The moulting process takes a few weeks during which they seldom go to sea; at other times of the year elephant seals are pelagic in mostly ice free waters (Bonner 1990, Borneman *et al.* 2000). Elephant seals feed on squid and fish, including toothfish (summarized in Hindell *et al.* 2003). They are preyed upon by killer whales (Keith *et al.* 2001), and in sub-Antarctic latitudes by white sharks (*Carcharodon carcharias*; van der Hoff & Morrice 2008).

We predict that southern elephant seals may benefit from regional climate change. Warming in the Antarctic Peninsula, with disappearance of sea ice as well as retreat of ice fields and glaciers, has already created additional beach areas for moulting, pupping and breeding and their populations are expanding into these areas, e.g. on Anvers Island (Fig. 2b; seals vs year, $r_s = 0.454$, $P < 0.02$). The relationship between seals and ice extent and ice area is inverse ($r_s = -0.221$, $r_s = -0.257$), but statistically weak, indicating that other factors besides large-scale sea ice are involved in trends. Establishment of breeding at Arthur Harbour, Anvers Island, as was the case in the re-invasion of the northern elephant seal's (*M. angustirostris* (Gill)) former colonies, began with several years of increasing numbers of moulting individuals (e.g. LeBoeuf *et al.* 1974, for a particularly well documented case). Although the evidence is somewhat controversial, elephant seals may have bred on the coast of Victoria Land during a warm period in the mid-Holocene (Hall *et al.* 2006). We have indicated (Table I) favourable reactions to decreases in the first five factors dealing with loss of sea ice and shelf ice, which will result in the exposure of more beach areas. The major uncertainty here is how changes in the Antarctic food webs will influence their populations.

Fur seal

The Antarctic fur seal (and closely related taxa) breeds on sand or cobbled beach as well as on rocky headlands at South Georgia, Macquarie, Heard, Kerguelen and the South Shetland islands (Condy 1978b). Adult males hold territories, beginning October to December, and may have 10–120 females within the defended boundaries. Females give birth within these territories over a three-week period in November and December, suckling the pup intermittently for four months and making repeated trips to sea to feed (Robinson *et al.* 2002, Kirkman *et al.* 2003b). Females enter the period of oestrus 6–7 days after giving birth. Fur seals during the non-breeding season are pelagic for long periods; in higher latitudes males, especially, haulout regularly on beaches (e.g. Riedman 1990, Green *et al.* 1991, Daneri & Coria 1992). Antarctic fur seals feed on krill (at high latitudes), myctophid fish, and mackerel icefish (*Champsocephalus gunnari* Lönnberg) in near-surface waters (Green *et al.* 1989, Goldsworthy *et al.* 1997, Klages & Bester 1998, Reid *et al.* 2005, Murphy *et al.* 2007). The lanternfish are caught during night when the fish rise to near the surface. During their pelagic phase, individuals in the high latitudes haulout on ice floes near the large-scale edge of the sea ice (Ribic *et al.* 1991).

Antarctic fur seals at high latitudes will probably be disadvantaged the most from the lack of krill offshore of their pupping and breeding beaches. At South Georgia foraging energetics and pup survival have been shown to depend on the availability of krill for foraging females during lactation (e.g. Costa *et al.* 1989, Forcada *et al.* 2005). Thus, we have predicted that changes in the food web will have the most effect on this species. At Anvers Island, the fur seals have been increasing ($r_s = 0.719$, $P < 0.001$). As with elephant seals there, the relationship to ice extent and area is inverse but weak ($r_s = -0.390$, $r_s = -0.261$) indicating other factors are also involved in the trends and probably could involve krill prevalence. At lower latitudes, fur seals prey heavily on fish (references above), which increases our uncertainty about the effect of lower krill availability over the long term. Loss of sea ice is predicted to have little effect (except as previously noted via its negative consequences on krill abundance), but increased beach availability could provide additional pupping and breeding areas (Table I).

Discussion

Each of the Antarctic pack ice seals relies on certain species-specific sea ice characteristics to complete its annual cycle as part of its respective life-history strategy (Erickson *et al.* 1971, Gilbert & Erickson 1977). Our predictions about probable sensitivity to climate-change related alterations in habitat (Table I) suggest that the crabeater seal will be the most affected, with the Weddell seal following closely behind. Any environmental change that would decrease the size and thickness of floes (IPCC 2007) would probably increase competition among (and predation on) seals, especially crabeaters because females require floes that do not melt before the period of lactation is complete.

Fig. 3. A beach scene that includes four species of seals (Weddell, elephant, leopard, and fur), that was photographed at Seal Island in the Antarctic Peninsula Region. This scene is probably a look into the future of seal habitat use as sea ice areas decline. (Photo: John L. Bengtson)

Leopard and Ross seals may be less influenced by these factors and we suggest that changes in sea ice extent, thickness or persistence will have little effect on the two ice-tolerant species; however, this is suggested without implying major changes in their food resources. The mix of species depicted in Fig. 3 illustrates a possible look into the future, and what we might expect as sea ice diminishes. More beach space, unless decreased by rising sea levels, will become available, but the competition for this space will become more intense. Further, this picture depicts that the crabeater, because of its especially strong reliance on sea ice, and the Ross seal, because of its pelagic nature, will probably not adapt, or lose out in the competition among species for the use of beach space to satisfy life-history needs. Learmonth *et al.* (2006) briefly consider the Antarctic seals in their review of effects of climate change on marine mammals. Our findings are similar to theirs (as presented in their Table I), but differ in details about the species involved. They suggest, incorrectly (p. 452), that Weddell, crabeater, and Ross seals are highly philopatric, and thus will be severely affected. However, both the crabeater and the Ross seal carry out pupping and breeding in the drifting pack ice. Thus, only the Weddell, as is evident in their response to the 'iceberg natural experiment' (see Results), will probably be affected by loss of site-specific breeding locations.

Prey, other than krill, has seldom been recorded for crabeater seals and Antarctic krill is an important component of the diet of Antarctic fur seals in the Scotia Sea region, particularly during the period of lactation. As the sea ice in continental slope regions becomes less extensive or persistent, Antarctic krill abundance probably will diminish (Fraser & Hoffman 2003, Atkinson *et al.* 2005) and, hence, food shortages for these pinnipeds may occur (see also Murphy *et al.* 2007). Given that neritic areas are rather limited in the Antarctic, any increase in persistence and size of coastal polynyas, and resulting increases in crystal krill, probably cannot make up for the loss of Antarctic krill, at least in regard to the large scale of seal population change. Indirectly, then, although there is uncertainty in the degree to which they can switch to fish, such as myctophids in the case of fur seals, changes in food availability will probably have an important net effect. We hypothesize that the reversing trend in fur seal numbers at Arthur Harbour after 1993 (Fig. 2b) is related, at least in part, to the decline in krill that has been observed in this region (cf. Atkinson *et al.* 2005). An inflection point in population trajectory of fur seals at South Georgia, with the population there initially recovering from exploitation but then declining, occurred at about the same time as that at Arthur Harbour. Reid & Croxall (2001) attributed the pattern at South Georgia to a change in the availability of krill in the region.

The Weddell seal is the other species that is highly sensitive to changes in sea ice. Both decreasing and increasing fast ice extent and thickness influence pupping success in this species. The decline in sea ice persistence in the Peninsula region seems to have negatively affected this species, as did the short-term increase in fast ice thickness and extent in McMurdo Sound. This two-sided pattern is analogous to the relationship between pack ice and Adélie penguins (*Pygoscelis adeliae* (Hombron & Jacquinot)), wherein too much or too little sea ice has negative effects on population dynamics and occurrence (Fraser & Trivelpiece 1996, Smith *et al.* 1999). Decrease in the persistence of fast ice has been documented to negatively affect the Antarctic's other fast ice breeding vertebrate, the emperor penguin (cf. Barbraud & Weimirskirch 2001, Ainley *et al.* 2005b).

Over the past recent decades, changing climate patterns have been very different in different sectors of the Antarctic (e.g. Zwally *et al.* 2002, Parkinson 2002, Stammerjohn *et al.* 2008). Overall, large, contrasting changes in the distribution and abundance of seals should have resulted. As shown by Weddell seals in the McMurdo region, their responses to sea ice change can be rapid. Cascading effects may also occur, where some dominant physical change could cause major shifts at several ecosystem levels. For instance, declining sea ice presence off the western Antarctic Peninsula has not only affected the physical environment but the food web as well (Emslie & McDaniel 2002, Atkinson *et al.* 2005, Ducklow *et al.* 2007).

For the elephant and fur seals their critical habitat needs involve breeding/pup-rearing space and food. As ice shelves disintegrate ever farther south, but more importantly as sea ice recedes, these ice tolerant species should continue to expand southward, as evidenced by the population trends observed at Arthur Harbour and in Marguerite Bay (see also Hall *et al.* 2006).

Although changing climate has altered the susceptibility of marine mammals to disease in warmer regions (Gian-Reto *et al.* 2002, Ross 2002, Ward & Lafferty 2004), at present there is no way to gauge the potential for this effect in the Antarctic.

One important potential confounding factor to predicting future trends in Antarctic pinniped populations is the profound alteration of food webs that has occurred or is occurring by industrial fishing (e.g. Gon & Heemstra 1990, Kock 1992, Pauly *et al.* 1998, 2005, Worm & Meyers 2003, Ainley *et al.* 2007). Food-web alterations owing to fish depletion may have been as important as climate-change effects for some seal species, thus in our opinion complicating study of climate change effects on Southern Ocean vertebrates. The mackerel ice fish, an important prey of fur seals, elephant seals and other top predators, was long ago seriously depleted from lower-latitude sites (e.g. Gon & Heemstra 1990, Kock 1992, Reid *et al.* 2006, Lescroël & Bost 2006), probably reducing the diet options for these predators. Whether or not a greater reliance on krill in recent decades has become a factor in the increased responses of these species to climate change will not soon be known. Moreover, and unfortunate for the investigation of climate effects on Weddell seals, commercial fisheries have recently begun to exploit the Antarctic toothfish in the Ross Sea (Ainley *et al.* 2006). Such commercial ventures will no doubt complicate future interpretations of the causes of change in Antarctic seal populations.

Finally, we fully realize that the projections we have made about the future fate of the Antarctic seals are mostly guesses based on our combined Antarctic experiences and observations, and on the data that have been collected as certain environmental events have taken place. Therefore, we welcome comments others might have about these predictions of future trends.

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References

Ackley, S.F., Bengtson, J.L., Boveng, P., Castellini, M., Daly, K.L., Jacobs, S., Kooyman, G.L., Laake, J., Quetin, L., Ross, R., Siniff, D.B., Stewart, B.S., Stirling, I., Torres, J. & Yochem, P.K. 2003. A top-down, multidisciplinary study of the structure and function of the pack ice ecosystem in the eastern Ross Sea, Antarctica. *Polar Record*, **39**, 219–230.

Ainley, D.G., Ballard, G., Karl, B.J. & Dugger, K.T. 2005a. Leopard seal predation rates at penguin colonies of different size. *Antarctic Science*, **17**, 335–340.

Ainley, D.G., Clarke, E.D., Arrigo, K., Fraser, W.R., Kato, A., Barton, K.J. & Wilson, P.R. 2005b. 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., Toniolo, V., Ballard, G., Barton, K., Eastman, J., Karl, B., Focardi, S., Kooyman, G., Lyver, P., Olmastroni, S., Stewart, B.W., Testa, W.P. & Wilson, P. 2006. Managing ecosystem uncertainty: critical habitat and dietary overlap of top-predators in the Ross Sea. *CCAMLR WG-EMM-06/29*, Hobart, Australia.

Ainley, D.G., Ballard, G., Blight, L., Eastman, J.T., Lescröel, A., Olmastroni, S., Townsend, S.E., Wilson, P.R. & Woehler, E. 2007. Paradigm lost, or is top-down forcing no longer an element of the Antarctic marine ecosystem? *Antarctic Science*, **19**, 283–290.

Arrigo, K.R. & Van Dijken, G.L. 2004. Annual changes in sea ice, chlorophyll *a*, and primary production in the Ross Sea, Antarctica. *Deep Sea Research II*, **51**, 117–138.

Arrigo, K.R., Van Dijken, G.L., Ainley, D.G., Fahnestock, M.A. & Markus, T. 2002. The impact of the B-15 iceberg on productivity and penguin breeding success in the Ross Sea, Antarctica. *Geophysical Research Letters*, **29** (7), 10.1029/2001GL014160.

Atkinson, A., Siegel, V., Pakhomov, E. & Rothery, P. 2005. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature*, **432**, 100–103.

Barbraud, C. & Weimerskirch, H. 2001. Emperor penguins and climate change. *Nature*, **411**, 183–186.

Bester, M. & Hofmeyr, G. 2007. Seals. *In* Riffenburgh, B., *ed. Encyclopedia of the Antarctic*. New York: Taylor & Francis, 877–880.

Bester, M.N. & Odendaal, P.N. 2000. Abundance and distribution of Antarctic pack ice seals in the Weddell Sea. *In* Davison, W., Howard-Williams, C. & Broady, P., *eds. Antarctic ecosystems: models for wider ecological understanding.* Christchurch: Caxton Press, 51–55.

Bester, M.N., Hofmeyr, G.J.G., Kirkman, S.P., Chauke, L.F., De Bruyn, P.J.N., Ferreira, S.M., Makhado, A.B., Maswime, T.A.M., McIntyre, K.T., Mulaudzi, T.W., Munyai, F.M., Pistorius, P.A., Radzilani, P.M., Ramunasi, A.J., Tshithabane, N.H. & Wilkinson, I.S. 2006. The leopard seal at Marion Island, vagrant or seasonal transient? *South African Journal of Wildlife Research*, **36**, 195–198.

Blix, A.S. & Nordoy, E.S. 2007. Ross seal (*Ommatophoca rossii*) annual distribution, diving behavior, breeding and moulting, off Queen Maud Land, Antarctica. *Polar Biology*, **30**, 1449–1458.

Bonner, W.N. 1985. Impact of fur seals on the terrestrial environment at South Georgia. *In* Siegfried, W.R., Condy, P.R. & Laws, R.M., *eds. Antarctic nutrient cycles and food webs.* Berlin: Springer, 641–646.

Bonner, W.N. 1990. *The natural history of seals.* New York: Facts on File Press, 196 pp.

Bornemann, H., Kreyscher, M., Ramdohr, S., Martin, T., Carlini, A.R., Sellmann, L. & Plötz, J. 2000. Southern elephant seal movements and Antarctic sea ice. *Antarctic Science*, **12**, 3–15.

Burns, J.M., Castellini, M.A. & Testa, J.W. 1999. Movements and diving behavior of weaned Weddell seal (*Leptonychotes weddellii*) pups. *Polar Biology*, **21**, 23–36.

Burns, J.M., Trumble, S.J., Castellini, M.A. & Testa, J.W. 1998. The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. *Polar Biology*, **19**, 272–282.

Boyd, I.L. 1993. Pup production and distribution of breeding Antarctic fur seals (*Arctocephalus gazella*) at South Georgia. *Antarctic Science*, **5**, 17–24.

Cameron, M.F. & Siniff, D.B. 2004. Age-specific survival, abundance, and immigration rates of a Weddell seal (*Leptonychotes weddellii*) population in McMurdo Sound, Antarctica. *Canadian Journal of Zoology*, **82**, 601–615.

Condy, P.R. 1978a. The distribution and abundance of southern elephant seals, *Mirounga leonina*, on the Prince Edward Islands. *South African Journal of Antarctic Research*, **8**, 42–48.

Condy, P.R. 1978b. The distribution, abundance and annual cycle of fur seals *Arctocephalus* spp. on the Prince Edward Islands. *South African Journal of Wildlife Research*, **8**, 159–168.

Condy, P.R. 1979. Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.), at Marion Island. *South African Journal of Zoology*, **14**, 95–102.

Costa, D.P., Croxall, J.P. & Duck, D. 1989. Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology*, **70**, 596–606.

Croxall, J.P. 1992. Southern ocean environmental changes: effects on seabird, seal and whale populations. *Philosophical Transactions of the Royal Society of London*, **B338**, 319–328.

Croxall, J.P., Trathan, P.N. & Murphy, E.J. 2002. Environmental change and Antarctic seabird populations. *Science*, **297**, 1510–1514.

Danieri, G.A. & Coria, N.R. 1992. The diet of Antarctic fur seals, *Arctocephalus gazella*, during the summer-autumn period at Mossman Peninsula, Laurie Island (South Orkneys). *Polar Biology*, **11**, 565–566.

Dayton, P.K. 1989. Interdecadal variation in an Antarctic sponge and its predators from oceanographic climate shifts. *Nature*, **245**, 1484–1486.

Ducklow, H.W., Baker, K., Martinson, D.G., Quetin, L.B., Ross, R.M., Smith, R.C., Stammerjohn, S.E., Vernet, M. & Fraser, W. 2007. Marine pelagic ecosystems: the West Antarctic Peninsula. *Philosophical Transactions of the Royal Society of London*, **B362**, 67–94.

Emslie, S.D. & McDaniel, J.D. 2002. Adélie penguin diet and climate change during the middle to late Holocene in northern Marguerite Bay, Antarctic Peninsula. *Polar Biology*, **25**, 222–229.

Erickson, A.W., Siniff, D.B., Cline, D.R. & Hofman, R. 1971. Distributional ecology of Antarctic seals. *In* Deacon, G., *ed. Symposium on Antarctic ice and watermasses*. Cambridge: SCAR, 55–75.

Forcada, J., Trathan, P.N., Reid, K. & Murphy, E.J. 2005. The effects of global climate variability in pup production of Antarctic fur seals. *Ecology*, **86**, 2408–2417.

Fraser, W.R. & Hofmann, E.E. 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Marine Ecology Progress Series*, **265**, 1–15.

Fraser, W.R. & Trivelpiece, W.Z. 1996. Factors controlling the distribution of seabirds: winter-summer heterogeneity in the distribution of Adélie penguin populations. *Antarctic Research Series*, **70**, 257–272.

Gian-Reto, W., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Gilbert, J.R. & Erickson, A.W. 1977. Distribution and abundance of seals in the pack ice of the Pacific sector of the Southern Ocean. *In* Llano, G.A., *eds. Adaptations within Antarctic ecosystems*. Washington, DC: Smithsonian Institution, 703–740.

Goldsworthy, S.D., Hindell, M.A. & Crowley, H.M. 1997. Diet and diving behaviour of sympatric fur seals *Arctocephalus gazella* and *A. tropicalis* at Macquarie Island. *In* Hindell, M.A. & Kemper, C., *eds. Marine mammal research in the Southern Hemisphere.* Vol. 1. *Status*, *ecology and medicine*. Chipping Norton: Surrey Beatty, 151–163.

Gon, O. & Heemstra, P.C. 1990. *Fishes of the Southern Ocean.* Grahamstown, South Africa: J.L.B. Smith Institute of Ichthyology, 462 pp.

Green, K., Burton, H.R. & Williams, R. 1989. The diet of Antarctic fur seals *Arctocephalus gazella* (Peters) during the breeding season at Heard Island. *Antarctic Science*, **1**, 317–324.

Green, K., Williams, R. & Burton, H. 1991. The diet of the Antarctic fur seals *Arctocephalus gazella* during the late autumn and early winter around Heard Island. *Antarctic Science*, **3**, 359–361.

Hadley, G.L. 2006. *Recruitment probabilities and reproductive costs for Weddell seals in Erebus Bay*, *Antarctica.* PhD thesis, Montana State University, Bozeman, 128 pp. [Unpublished].

Hadley, G.L., Rotella, J.J. & Garrott, R.A. 2007a. Evaluation of reproductive costs for Weddell Seals in Erebus Bay, Antarctica. *Journal of Animal Ecology*, **76**, 448–458.

Hadley, G.L., Rotella, J.J. & Garrott, R.A. 2007b. Influence of maternal characteristics and oceanographic conditions on survival and recruitment probabilities of Weddell seals. *Oikos* **116**, 601–613.

Hall, B.L., Hoelzel, A.R., Baroni, C., Denton, G.H., Le Boeuf, B.J., Overturf, B. & Töpf, A.L. 2006. Holocene elephant seal distribution implies warmer-than-present climate in the Ross Sea. *Proceedings of the National Academy of Sciences of the United States*, **103**, 10213–10217.

Hindell, M.A., Bradshaw, C.J.A., Sumner, M.D., Michael, K.J. & Burton, H.R. 2003. Dispersal of female elephant seals and their prey consumption during austral summer: relevance to management and oceanographic zones. *Journal of Animal Ecology*, **40**, 703–715.

Hiruki, L.M., Schwartz, M.K. & Boveng, P.L. 1999. Hunting and social behaviour of leopard seals (*Hydrurga leptonyx*) at Seal Island, South Shetland Islands, Antarctica. *Journal of Zoology London*, **249**, 97–109.

Ingolfsson, O., Hjort, C., Berkman, P.A., Bjorck, S., Colhoun, E., Goodwin, I.D., Hall, B., Hirakawa, K., Melles, M., Moller, P. & Prentice, M.L. 1998. Antarctic glacial history since the last glacial maximum: an overview of the record on land. *Antarctic Science*, **10**, 326–344.

IPCC. 2007. *Climate Change 2007 - the physical science basis*. Ch. 4. Observations: snow, ice and frozen ground. Cambridge: Cambridge University Press, 337–385.

Jacobs, S. 2006. Observations of change in the Southern Ocean. *Philosophical Transactions of the Royal Society*, **A364**, 1657–1681.

Jacobs, S.S. & Comiso, J.C. 1989. Sea ice and oceanic processes on the Ross Sea continental shelf. *Journal of Geophysical Research*, **94**, 18195–18211.

Jacobs, S.S. & Giulivi, C.F. 1998. Interannual ocean and sea ice variability in the Ross Sea. *Antarctic Research Series*, **75**, 135–150.

Jonker, F.C. & Bester, M.N. 1994. The diving behaviour of adult southern elephant seal, *Mirounga leonina*, cows from Marion Island. *South African Journal of Antarctic Research*, **24**, 75–93.

Keith, M., Bester, M.N., Bartlett, P.A. & Baker, D. 2001. Killer whales (*Orcinus orca*) at Marion Island, Southern Ocean. *African Zoology*, **36**, 163–175.

Kim, S.L., Conlan, K., Malone, D.P. & Lewis, C.V. 2005. Possible food caching and defense in the Weddell seal: observations from McMurdo Sound, Antarctica. *Antarctic Science*, **17**, 71–72.

Kirkman, S.P., Bester, M.N., Pistorius, P.A., Hofmeyr, G.J.G., Jonker, F.C., Owen, R. & Stryydom, N. 2003a. Variation in the timing of moult in southern elephant seals at Marion Island. *South African Journal of Wildlife Research*, **33**, 79–84.

Kirkman, S.P., Bester, M.N., Makhado, A.B. & Pistorius, P.A. 2003b. Female attendance patterns of Antarctic fur seals at Marion Island. *African Zoology*, **38**, 402–405.

Kirkman, S.P., Bester, M.N., Hofmeyr, G.J.G., Jonker, F.C., Pistorius, P.A., Owen, R. & Stryydom, N. 2004. Variation in the timing of the breeding haulout of female southern elephant seals at Marion Island. *Australian Journal of Zoology*, **52**, 379–388.

Klages, N.T.W. & Bester, M.N. 1998. The fish prey of fur seals *Arctocephalus* spp. at subantarctic Marion Island. *Marine Biology*, **131**, 559–566.

Kock, K.-H. 1992. *Antarctic fish and fisheries.* Cambridge: Cambridge University Press, 359 pp.

Kooyman, G.L. 1965. Leopard seals of Cape Crozier. *Animals*, **6**, 59–63.

Laidre, K.L., Stirling, I., Lowry, L.F., Wiig, Ø., Heide-Jørgensen, M.-P. & Ferguson, S.H. In press. Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecological Applications.*

La Mesa, M., Eastman, J.T. & Vacchi, M. 2004. The role of notothenioid fish in the food web of the Ross Sea shelf waters: a review. *Polar Biology*, **27**, 321–338.

Laws, R.M. 1956. The elephant seal (*Mirounga leonina* Linn.). II. General, social and reproductive behaviour. *Falkland Islands Dependencies Survey*, *Scientific Reports*, No. 13, 1–88.

Laws, R.M. 1977. The significance of vertebrates in the Antarctic marine ecosystem. *In* Llano, G.A., *ed. Adaptations within Antarctic ecosystems.* Washington, DC: Smithsonian Institution, 411–438.

Learmonth, J.A., Macleod, C.D., Santos, G.L., Pierce, M.B., Crick, H.Q.P. & Robinson, R.A. 2006. Potential effects of climate change on marine mammals. *Oceanography and Marine Biology*, **44**, 431–464.

LeBoeuf, B.J., Ainley, D.G. & Lewis, T.J. 1974. Elephant seals on the Farallones: population structure of an incipient breeding colony. *Journal of Mammology*, **55**, 370–385.

Ledley, T.S. 1997. A possible ENSO signal in the Ross Sea. *Geophysical Research Letters*, **24**, 3253–3256.

Lescroël, A. & Bost, C.-A. 2006. Recent decrease in gentoo penguin populations at Iles Kerguelen. *Antarctic Science*, **18**, 171–174.

Matthews, L.H. 1977. *Penguins, whalers and sealers: a voyage of discovery.* New York: Universe Books, 165 pp.

McMahon, C.R. & Burton, H.R. 2005. Climate change and seal survival: evidence for environmentally mediated changes in elephant seal, *Mirounga leonina*, pup survival. *Proceedings of the Royal Society of London*, **B272**, 923–928.

Murphy, E.J., Watkins, J.L., Trathan, P.N., Reid, K., Meredith, M.P., Thorpe, S.E., Johnston, N.M., Clarke, A., Tarling, G.A., Collins, M.A., Forcada, J., Shreeve, R.S., Atkinson, A., Korb, R., Whitehouse, M.J., Ward, P., Rodhouse, P.G., Enderlein, P., Hirst, A.G., Martin, A.R., Hill, S.L., Staniland, I.J., Pond, D.W., Briggs, D.R., Cunningham, N.J. & Fleming, A.H. 2007. Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill centered food web. *Philosophical Transactions of the Royal Society*, **B362**, 113–148.

Nordøy, E.S. & Blix, A.S. 2001. The previously pagophilic Ross seal is now rather pelagic. *Proceeding VIII International Biology Symposium*, Amsterdam, the Netherlands, August 27–September 1, S5014.

Pakhomov, E.A. & Perissinotto, R. 1996. Antarctic neritic krill *Euphausia crystallorophias*: spatio-temporal distribution, growth and grazing rates. *Deep-Sea Research I*, **43**, 59–87.

Parkinson, C.L. 2002. Trends in the length of the Southern Ocean sea ice season, 1979–99. *Annals of Glaciology*, **34**, 435–440.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres Jr, F. 1998. Fishing down marine food webs. *Science*, **279**, 860–863.

Pauly, D., Watson, R. & Alder, J. 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. *Philosophical Transaction of the Royal Society of London*, **B360**, 5–12.

Pitman, R.L. & Ensor, P. 2003. Three forms of killer whales (*Orcinus orca*) in Antarctic waters. *Journal of Cetacean Research and Management*, **5**, 1–9.

Ponganis, P.J. & Stockard, T.K. 2007. The Antarctic toothfish: How common a prey for Weddell Seals? *Antarctic Science*, **19**, 441–442.

Proffitt, K.M., Garrott, R.A., Rotella, J.J., Siniff, D.B. & Testa, J.W. 2007. Exploring linkages between abiotic oceanographic processes and a top-trophic predator in an Antarctic ecosystem. *Ecosystems*, **10**, 119–126.

Reid, K. & Croxall, J.P. 2001. Environmental response of upper trophic level predators reveals a system change in an Antarctic marine ecosystem. *Proceedings of the Royal Society of London*, **B268**, 377–384.

Reid, K., Davis, D. & Staniland, I.J. 2006. Spatial and temporal variability in the fish diet of the Antarctic fur seal (*Arctocephalus gazella*) in the Atlantic sector of the Southern Ocean. *Canadian Journal of Zoology*, **84**, 1025–1037.

Reid, K., Hill, S.L., Diniz, T.C.D. & Collins, M.A. 2005. Mackerel ice fish *Champsocephalus gunnari* in the diet of upper trophic level predators at South Georgia: implications for fisheries management. *Marine Ecology Progress Series*, **305**, 153–161.

Ribic, C.A., Fraser, W.R. & Ainley, D.G. 1991. Habitat selection by marine mammals in the marginal ice zone. *Antarctic Science*, **3**, 181–186.

Riedman, M. 1990. *The pinnipeds, seals, sea lion, and walruses.* Berkeley, CA: University of California Press, 439 pp.

Robinson, S.A., Goldsworthy, S.G., Van Den Hoff, J. & Hindell, M.A. 2002. The foraging ecology of two sympatric fur seal species, *Arctocephalus gazella* and *Arctocephalus tropicalis*, at Macquarie Island during the austral summer. *Marine and Freshwater Research*, **53**, 1071–1082.

Rogers, T., Hogg, C. & Irvine, A. 2005. Spatial movement of adult leopard seals (*Hydrurga leptonyx*) in Prydz Bay, eastern Antarctica. *Polar Biology*, **28**, 456–463.

Ross, P.S. 2002. The role of immunotoxic environmental contaminants in facilitating the emergence of infectious diseases in marine mammals. *Human and Ecological Risk Assessment*, **8**, 277–292.

Russell, J.L., Dixon, K.W., Gnanadesikan, A., Stouffer, R.J. & Toggweiler, J.R. 2006. The Southern Hemisphere westerlies in a warming world: propping open the door to the deep ocean. *Journal of Climate*, **19**, 6382–6390.

Siniff, D.B. & Bengtson, J.L. 1977. Observations and hypotheses concerning the interactions among crabeater seals and leopard seals and killer whales. *Journal of Mammalogy*, **58**, 414–416.

Siniff, D.B., Stirling, I., Bengtson, J.L. & Reichle, R.A. 1979. Social and reproductive behaviour of crabeater seals (*Lobodon carcinophagus*) during the austral spring. *Canadian Journal of Zoology*, **57**, 2243–2255.

Siniff, D.B. & Stone, S. 1985. The role of the leopard seal in the trophodynamics of the Antarctic marine ecosystem. *In* Siegfried, W.R., Condy, P.R. & Laws, R.M., *eds. Antarctic nutrient cycles and food webs.* Berlin: Springer, 498–515.

Smith, R.C., Ainley, D., Baker, K., Domack, E., Emslie, S., Fraser, B., Kennett, J., Leventer, A., Mosley-Thompson, E., Stammerjohn, S. & Vernet, M. 1999. Marine ecosystem sensitivity to climate change. *BioScience*, **49**, 393–404.

Smith, T.G., Siniff, D.B., Reichle, R. & Stone, S. 1981. Coordinated behavior of killer whales (*Orcinus orca*) hunting a crabeater seal, *Lobodon carcinophagus*. *Canadian Journal of Zoology*, **59**, 1185–1189.

Stammerjohn, S.E., Martinson, D.G., Smith, R.C., Yuan, X. & Rind, D. 2008. Trends in Antarctic annual sea ice retreat and advance and their relation to ENSO and Southern Annular Mode variability. *Journal of Geophysical Research*, **113**, 10.1029/2007JC004239.

Stirling, I. & Parkinson, C.L. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. *Arctic*, **59**, 261–275.

Testa, J.W., Oehlert, G., Ainley, D.J., Bengston, J.L., Siniff, D.B., Laws, R.M. & Rounsevell, D. 1991. Temporal variability in Antarctic marine ecosystems: periodic fluctuations in the phocid seals. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 631–639.

Testa, J.W., Siniff, D.B., Croxall, J.P. & Burton, H.R. 1990. A comparison of reproductive parameters among three populations of Weddell seals (*Leptonychotes weddellii*). *Journal of Animal Ecology*, **59**, 1165–1175.

Thomas, J., Demaster, D., Stone, S. & Andriashek, D. 1980. Observations of a newborn Ross seal pup (*Ommatophoca rossi*) near the Antarctic Penninsula. *Canadian Journal of Zoology*, **58**, 2156–2158.

Van Den Hoff, J. & Morrice, M.G. 2008. Sleeper shark (*Somniosus antarcticus*) and other bite wounds observed on southern elephant seals (*Mirounga leonina*) at Macquarie Island. *Marine Mammal Science*, **24**, 239–247.

Visser, I.N., Smith, T.G., Bullock, I.D., Green, G.D., Carlsson, O.G.L. & Imberti, S. 2008. Antarctic peninsula killer whales (*Orcinus orca*) hunt seals and a penguin on floating ice. *Marine Mammal Science*, **24**, 225–234.

Ward, J.R. & Lafferty, K.D. 2004. The elusive baseline of marine disease: are diseases in ocean ecosystems increasing? *PLoS Biology*, **2**, e120.

Weimerskirch, H., Inchausti, P., Guinet, C. & Barbraud, C. 2003. Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarctic Science*, **15**, 1–8.

Worm, B. & Meyers, R.A. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology*, **84**, 162–173.

Zwally, H.J., Comiso, J.C., Parkinson, C.L., Cavalieri, D.J. & Gloersen, P. 2002. Variability of Antarctic sea ice 1979–1998. *Journal of Geophysical Research*, **107**, 10.1029/2000JC000733.