A REVIEW OF DATA ON ABUNDANCE, TRENDS IN ABUNDANCE, HABITAT USE AND DIET OF ICE-BREEDING SEALS IN THE SOUTHERN OCEAN

C. Southwell✉
Australian Antarctic Division
Department of the Environment, Water, Heritage and the Arts
203 Channel Highway
Kingston, Tasmania 7050
Australia
Email – colin.southwell@aad.gov.au

J. Bengtson
National Marine Mammal Laboratory
NOAA Fisheries
7600 Sand Way Point, N.E.
Seattle, WA 98115
USA

M. Bester
Mammal Research Institute
Department of Zoology and Entomology
University of Pretoria
Pretoria 0002
South Africa

A. Schytte Blix
Department of Arctic Biology
University of Tromso
N-9037, Tromso
Norway

H. Bornemann
Alfred Wegener Institute
Postfach 120161
D-27515 Bremerhaven
Germany

P. Boveng and M. Cameron
National Marine Mammal Laboratory
NOAA Fisheries
7600 Sand Way Point, N.E.
Seattle, WA 98115
USA

J. Forcada
British Antarctic Survey
High Cross, Madingley Road
Cambridge CB3 0ET
United Kingdom

J. Laake
National Marine Mammal Laboratory
NOAA Fisheries
7600 Sand Way Point, N.E.
Seattle, WA 98115
USA

E. Nordøy
Department of Arctic Biology
University of Tromso
N-9037, Tromso
Norway

J. Plötz
Alfred Wegener Institute
Postfach 120161
D-27515 Bremerhaven
Germany

T. Rogers
School of Biological, Earth and Environmental Sciences
The University of New South Wales
Sydney
Australia

D. Southwell
Australian Antarctic Division
Department of the Environment, Water, Heritage and the Arts
203 Channel Highway
Kingston, Tasmania 7050
Australia

D. Steinhage
Alfred Wegener Institute
Postfach 120161
D-27515 Bremerhaven
Germany

B.S. Stewart
Hubbs-SeaWorld Research Institute
2595 Ingraham Street
San Diego, CA 92109
USA

P. Trathan
British Antarctic Survey
High Cross, Madingley Road
Cambridge CB3 0ET
UK

Abstract

The development of models of marine ecosystems in the Southern Ocean is becoming increasingly important as a means of understanding and managing impacts such as exploitation and climate change. Collating data from disparate sources, and understanding biases or uncertainties inherent in those data, are important first steps for improving ecosystem models. This review focuses on seals that breed in ice habitats of the Southern Ocean (i.e. crabeater seal, *Lobodon carcinophaga*; Ross seal, *Ommatophoca rossii*; leopard seal, *Hydrurga leptonyx*; and Weddell seal, *Leptonychotes weddellii*). Data on populations (abundance and trends in abundance), distribution and habitat use (movement, key habitat and environmental features) and foraging (diet) are summarised, and potential biases and uncertainties inherent in those data are identified and discussed. Spatial and temporal gaps in knowledge of the populations, habitats and diet of each species are also identified.

Introduction

The development of ecosystem models is becoming more important as a means of understanding and managing impacts (e.g. exploitation and climate change) in the Southern Ocean. Recently the Scientific Committees of two Commissions responsible for managing biota in the Southern Ocean (i.e. the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) and the International Whaling Commission (IWC)) recognised the importance of ecosystem modelling by convening a joint workshop to coordinate and improve the capacity of ecosystem modelling for both Commissions.

The focus of the workshop was on the data needed as input to ecosystem models rather than on the specifics of particular models. The data required for models of marine ecosystems cover many taxa, are scattered throughout the literature, and are likely to have many biases, uncertainties and gaps that could limit or affect the performances of those models. Assimilating those data and understanding any biases or uncertainties inherent in them are important first steps for improving ecosystem modelling. Identifying important gaps in knowledge can also focus data collection in the most needed areas.

This review focuses on seals that breed in the fast-ice and pack-ice habitats of the Southern Ocean (crabeater seal, *Lobodon carcinophaga*; Ross seal, *Ommatophoca rossii*; leopard seal, *Hydrurga leptonyx*; and Weddell seal, *Leptonychotes weddellii*). All four species of seal that breed in the sea-ice habitats of the Southern Ocean have circumpolar distributions and use the sea-ice as a platform to haul out on when giving birth and moulting. Breeding occurs in late spring and early summer, and moulting in mid- to late summer. For the rest of the year, these species spend much of their time foraging in the ocean, but continue to haul out periodically to rest, making them amenable to observe and count from the air or from ships. Crabeater, Ross and leopard seals usually occur alone or in small groups when hauled out, whereas Weddell seals often aggregate in larger groups in fast-ice habitats in early summer when breeding. Data on populations (abundance and trends in abundance), distribution and habitat use (movement, key habitat and environmental features) and foraging (diet) are summarised, potential biases and uncertainties inherent in the data are identified and discussed, and spatial and temporal gaps are identified.

Abundance

General survey methods

The general survey methods used to estimate abundance have been developed around the biological characteristics of the ice-breeding seals. Due to their dispersed distribution over very large areas, ships and aircraft have been used as vehicles to survey seals that are hauled out, using transects as sampling units, to first estimate densities of seals hauled out. Independent studies of haul-out behaviour are then needed to correct those estimates of density to total density, which is then converted to an estimate of abundance taking into account the area of sea-ice.

Survey reviews

The first regional and circumpolar estimates of abundance of Antarctic seals were reported in the late 1940s and early 1950s (Table 1). Laws (1953) estimated the abundances of the four species in the Falkland Island Dependencies, though he cautioned that those estimates were gross and largely guesses. They were evidently not based on the use of rigorous survey methods. Scheffer (1958) later estimated the circumpolar abundance of each species, but he did not describe the survey methods used to derive them. The first estimates that describe methods were reported by Eklund and Atwood (1962) and Eklund (1964). They made sightings from ships along transects in two relatively small areas of pack-ice in the Pacific and Indian Ocean sectors in December–January 1956/57 (Figure 1, methods summarised in Table 2). To derive circumpolar estimates of abundance, they applied the average density of seals hauled out along sample transects to the estimated area of pack-ice around Antarctica in January (Table 3), though they qualified this by noting that the two regional samples were inadequate to represent the entire pack-ice.

From the late 1960s to the early 1980s, Erickson and colleagues made a series of shipboard and aerial surveys around the Antarctic continent (Figure 2), and then derived several estimates of regional and circumpolar abundance for the four species (Tables 1, 2 and 3).

The earliest of those surveys were in the Weddell Sea in the austral summers of 1967/68, 1968/69 and 1969/70. Erickson et al. (1969) and Siniff et al. (1970) computed densities of crabeater seals seen hauled out during shipboard strip transects in the pack-ice of the Weddell Sea (Figure 2), but they did not estimate population sizes for the entire region because the relationship between the number of seals counted on the ice and the number actually present in the area was unknown (Siniff et al., 1970). Erickson et al. (1971) later reported the results of observational studies of haul-out patterns of crabeater seals relative to time of day during the 1968/69 surveys. They re-calculated crabeater seal densities, where appropriate, by adjusting counts of hauled-out seals upwards to the number expected at midday (i.e. 1100–1400 hr) peak haul-out time. They then applied the adjusted densities to the total estimated area of pack-ice in the Weddell Sea that was typical of having been surveyed to obtain an approximate estimate of the abundance of crabeater seals in the Weddell Sea (8.25 million in 1967/68 and 10.60 million in 1968/69; Table 1). Erickson et al. (1971) cautioned about some potential biases and errors in these approximate estimates (e.g. seals missed in surveys; the likely presence of seals in unsampled habitat such as ice-free areas or consolidated ice; errors in estimation of ice habitat), but nonetheless speculated about a circumpolar population of crabeater seals of between 50 and 75 million. The authors did not derive estimates of the abundances of Ross, leopard or Weddell seals, but noted that adjustments for haul-out would also have to be made for these species.

From 1970 to 1974, Erickson and his colleagues surveyed several other regions around Antarctica (Tables 2 and 3 and Figure 2), including the western Ross Sea region in 1970/71 (briefly mentioned by Erickson et al., 1971), the Amundsen–Bellingshausen Seas region (135°W–80°W) in 1971/72 (unadjusted or hauled-out densities reported in Erickson et al., 1972), the Oates and George V coast region (145°E–170°E) in 1972/73 (densities of seals hauled out and a minimum population estimate reported in Erickson et al., 1973), and the Adélie, Claire and BANZARE coast region (120°E–137°E) in 1973/74 (densities of seals hauled out reported in Erickson et al., 1974). All but the last of those surveys were analysed and presented in more detail in Gilbert and Erickson (1977), as summarised below.

In the western Ross Sea survey, seals were counted from vertical photographs taken from a fixed-wing aircraft flying along transects in November 1970 (Figure 2). Seals were not distinguished by species, the time of day that the photographs were taken was not indicated by Gilbert and Erickson (1977), and it is not clear whether counts were adjusted for haul-out patterns. Extrapolation of density in sampled strips to 919 000 km^2 of pack-ice (latitudinal and longitudinal bounds not specified) resulted in an estimate of 48 750 seals (Gilbert and Erickson, 1977; estimate not shown in Table 1 because it was not species-specific).

In the Amundsen–Bellingshausen Seas and Oates–George V coast surveys, counts were made and recorded directly from a helicopter flying at 152 m altitude along transects extending from the ice edge southward (Table 3, Figure 2). Because most of the pack-ice habitats in the inner region of the area could not be reached by the helicopter (Figure 2), aerial photographic surveys from a fixed-wing aircraft (similar to those in the western Ross Sea, above) were also made along two transects through the interior of the pack-ice. In both regions the helicopter surveys were made between 1100 and 1400 hr solar time when most crabeater seals were expected to be hauled out, and one observer counted seals within strips of 463 m width on each side of the helicopter. Densities of seals hauled out in the outer ice regions were calculated using strip transect methods, and densities were adjusted for haul-out patterns using a half-hourly time adjustment factor derived from counts from both surveys. The adjustment factor was apparently not species-specific. In the Oates–George V coast region, densities of seals in the interior of the pack-ice were derived from helicopter counts > 93 km south from the northern ice edge on the assumption that the nature of pack-ice was relatively constant from this point southward to the continent. In the Amundsen–Bellingshausen Seas region, densities of seals in the interior of the pack-ice were derived from a combination of helicopter counts > 130 km south from the northern ice edge and the aerial photography counts throughout the interior of the pack-ice. Separate estimates of abundance were calculated for outer and interior regions by extrapolating adjusted estimates of density across the estimated areas of pack-ice, and estimates for outer and interior regions were then summed to derive an estimated total population size for each species in each region (Table 1).

Collectively, Erickson's surveys from 1967/68 to 1973/74 between 25°W and 120°E covered slightly more than half the circumpolar pack-ice region (Figure 2). A final effort during a circumpolar voyage around Antarctica in the summer of 1982/83 (Erickson et al., 1983) was made to sample the sea-ice off the other half of the continent to allow estimates of circumpolar population abundance for each species to be made (Erickson and Hanson, 1990). The survey effort in 1982/83 involved both aerial and shipboard surveys (only aerial transects are shown in Figure 2 as shipboard transects were not described by Erickson et al. (1983)). As in previous aerial surveys, transects were flown directly southward from the outer ice edge and seals were counted by one observer within 463 m wide strips on each side of the helicopter. The surveys in 1982/83 were, however, flown at a substantially lower altitude (76 m vs. 152 m in earlier surveys). Shipboard survey methods were the same as those used in previous years. The area of interior ice that was covered by aerial surveys, and the location and distribution of shipboard transects in the pack-ice, were not described by Erickson et al. (1983). Only raw counts were presented by Erickson et al. (1983); analysis and synthesis of these data with all the data collected in previous years appears in Erickson and Hanson (1990), as summarised below.

The main features of the synthesis and revised analysis by Erickson and Hanson (1990) were the collection of additional data on haul-out patterns and the development and testing of a model to account for diurnal variation in counts of seals hauled out (Erickson et al., 1989). During the final circumpolar survey in 1982/83, crabeater seals hauled out on the ice were counted throughout the day from a relatively stationary position in the pack-ice at five locations around Antarctica in February (at one of these sites counts of Weddell seals were also made, and crabeater counts in 1969 were also available from a sixth location). Regression analysis indicated a unimodal distribution of counts that peaked around midday at all sites. A predictive model was then developed to adjust counts at any time of day to those expected at the time of peak haul-out. Erickson and Hanson (1990) applied this model to all counts made during the surveys from 1967/68 to 1982/83 and derived estimates of abundance for five oceanographic regions (Amundsen–Bellingshausen Seas (60°W–130°W), Ross Sea (130°W–160°W), south Pacific Ocean (90°E–160°E), south Indian Ocean (20°E–90°E) and Weddell Sea (20°E–60°W)). The haul-out model developed for crabeater seals in February was applied to counts of each species over the months of January to March. The revised estimates are shown in Table 1. The estimates of abundance from the reanalysis were generally lower than the original estimates, and substantially and surprisingly lower in some regions (e.g. 8.2–10.6 million for original estimates vs. 2.2 million for the reanalysis in the western Weddell Sea region; 1.19 million for original vs. 0.63 million for the reanalysis in the Amundsen–Bellingshausen Seas region). Based on the revised regional estimates, Erickson and Hanson (1990) estimated the circumpolar population of crabeater seals in unconsolidated pack-ice to be at least 7 million, though they stressed that this did not include the potentially significant number of seals that might be in ice-free areas of the Southern Ocean in summer, nor the number of seals that did not haul out during the peak haul-out period. From those considerations, they thought that a circumpolar population of 11–12 million crabeater seals was reasonable. Laws (1984) had earlier derived an estimate of around 15 million crabeater seals from the Erickson surveys from 1967/68 to 1972/73 (Table 1), but noted that this might have been conservative and had further speculated that a population of 30–40 million crabeater seals might not be unlikely.

Ainley (1985) carried out shipboard sighting surveys of seabirds and marine mammals in the Ross Sea in December and January in the austral summers of 1976/77, 1977/78 and 1979/80 (Table 2, Figure 3). The densities of seals hauled out in sampled areas were estimated using strip transect methods and then adjusted to the densities expected at the time of peak haul out in a manner similar to Erickson et al. (1971). Abundances were estimated for each of the four seal species in the surveyed region by constructing strata based on ice and physical attributes, calculating abundance in each strata as the product of average-adjusted density for each species and strata area, and finally summing the strata estimates for each species. The resulting estimates of abundance were 204 000 crabeater seals, 5 000 Ross seals, 8 000 leopard seals and 32 000 Weddell seals (Table 1).

The Antarctic Pack-Ice Seals (APIS) program was initiated by the Scientific Committee on Antarctic Research (SCAR) Group of Specialists on Seals. A key aim of the APIS program was to coordinate multiple ship and aerial operations to obtain a synoptic circumpolar survey effort. The APIS surveys also planned to implement improvements in methods to address some of the known or potential biases in earlier surveys.

It was not logistically possible to sample all areas of the Antarctic pack-ice in one year, but the resulting spatial coverage of the coordinated APIS program was substantially better in its geographic scope (both longitudinally and latitudinally) than all previous surveys (compare Erickson surveys in Figure 2 with the APIS surveys in Figure 4). Shipboard and aerial sighting surveys undertaken in the summer of 1999/2000 were contiguous and extended around half the continent from 100°W to 64°E (Figure 4). In the three previous summers, aerial surveys were carried out along the Antarctic Peninsula (1998/99) and eastern Weddell Sea coasts (1996/97 and 1997/98), and aerial photographic surveys were carried out over the pack-ice of the eastern Weddell Sea during five consecutive summers from 1996/97 to 2000/01 (Figure 4). The use of ship-based helicopters improved the north to south coverage of pack-ice.

In contrast to Erickson's aerial sighting surveys, where one observer counted in 463 m strips on each side of the aircraft and did not record distance data, observers in the APIS aerial surveys counted seals on only one side of the aircraft and recorded distance data to allow estimates of densities of seals hauled out to be made with line transect methods. Some aerial surveys also used additional observers to allow density to be estimated from mark-recapture line transect methods and testing of the line transect assumption of perfect detection on the transect line (Table 3). Line transect methods were also used during shipboard surveys (Table 2).

An integral component of the APIS work was the deployment of satellite-linked dive recorders on a sample of seals around the continent to estimate the probability of seals being hauled out at any time of day or year. Dive recorders were attached to seals of all four species and provided haul-out data throughout each day for several months or more (Bengtson and Cameron, 2004; Southwell, 2003, 2005; Blix and Nordøy, 2007; Nordøy and Blix, 2009). Those data allowed improved adjustment of counts of seals hauled out during the surveys relative to diel haul-out patterns, first by estimating the previously unknown proportion of seals in the water at the time of peak haul-out, second by estimating species-specific haul-out probabilities rather than assuming similar haul-out behaviour for all species, and third by estimating probability of haul-out specific to the time of year that each sighting survey was done.

Although the spatial coverage of pack-ice habitat by the APIS transects was more comprehensive than for previous surveys, the practical constraints on ship and aircraft operation in the pack-ice meant that true random or representative placement of transects was not possible. To address and minimise bias in extrapolating from densities of seals sampled along the potentially non-representative transects to the entire area of pack-ice, analysis of the APIS data used spatial modelling and predictive methods (Bengtson et al., 2011; Forcada and Trathan, 2008; Southwell et al., 2008a, 2008b, 2008c).

Analysis of the APIS data has addressed the major sources of uncertainty in estimating abundance. Bootstrap and jack-knife methods were used to include uncertainty related to the estimation of probabilities of detection and haul-out, and uncertainty in predicting abundance across the survey region using spatial models (Bengtson et al., 2011; Forcada and Trathan, 2008; Southwell, 2008a, 2008b, 2008c). Model uncertainty was considered by deriving estimates based on several plausible predictive models, and uncertainty related to species identification was addressed by estimating abundance from both definite only and definite plus probable species sightings. The problem of dynamic sea-ice distribution was addressed by deriving a survey region that represented the local sea-ice extent and concentration at the time that surveys were conducted (Bengtson et al., 2011).

Most regional analyses of APIS data have been completed. The most plausible estimates of crabeater seal abundance were 1 736 000 (95% CI 1 219 000–2 472 000) for the longitudinal sector from 150°E to 100°W, 3 187 000 (1 754 000–4 748 000) from 90°W to 30°W, and 946 000 (726 000–1 397 000) from 64°E to 150°E. The crabeater seal abundance estimate of 3 564 000 reported by Bester and Odendaal (2000) for the area from 26°W to 7°W was only a simple preliminary estimate and is likely to be an overestimate. Regional abundance estimates for Ross, leopard and Weddell seals were highly uncertain (150°E–100°W sector: Ross seals 22 600 (11 700–43 700); leopard seals 15 000 (3 500–65 000); Weddell seals

331 000 (144 000–759 000); 90°W–30°W sector: no estimate for Ross seals, only one seen; leopard seals 13 200 (3 700–23 100); Weddell seals 302 000 (77 000–576 000); 64°E–150°E sector: Ross seals 55 900 (27 700–187 500); leopard seals 7 300 (3 700–14 500); no estimate for Weddell seals because virtually no fast-ice was surveyed).

Potential biases and uncertainties in abundance estimates

Substantial biases and uncertainties were undoubtedly present in the early estimates of population size. Indeed the authors were very direct in stating the uncertainties known or suspected by them. The densities of seals hauled out reported by Eklund and Atwood (1962) would have underestimated true densities because no adjustment was made for the number of seals in the water at the time of the survey. The early circumpolar estimates were based on very limited sampling in two small regions of the circumpolar pack-ice, and there would be substantial uncertainty associated with extrapolating from the sampled regions to the entire pack-ice. Given these issues, the acknowledged guesswork underlying Laws' (1953) estimates, and the lack of information on survey methods for Scheffer's (1958) estimates, it is strongly recommended that all of these early estimates be treated only as the good-faith guesses that they were offered as.

The methods used during the Erickson surveys were an improvement over the early surveys. Nevertheless, there were several sources of actual or potential bias and uncertainty underlying the estimates derived from the Erickson surveys.

(i) Detectability. Use of strip transects would have resulted in a negative bias in estimates of densities of seals hauled out if some seals within the strips were undetected. This is very likely to have occurred during aerial surveys where a single observer searched across strips of 463 m width on both sides of the aircraft, but is unlikely in shipboard surveys using 200 m strips.

(ii) Correction for haul-out. Because correction of counts to peak haul-out was based only on counts of seals hauled out, the proportion of seals in the water at the time of peak haul-out could not be assessed and so was not accounted for. Recent studies using electronic dive recorders indicate that, for crabeater seals, the proportion of seals underwater around solar midday in the summer months is between 20% and 40% (Bengtson and Cameron, 2004; Bengtson et al., 2011; Southwell, 2005). Some more subtle biases in Erickson and Hanson's (1990) estimates may have arisen due to their use of haul-out adjustments developed only, or predominantly, for crabeater seals in February being applied to counts of all four species across the months of January to March. More recent studies have shown that haul-out behaviour varies among species and months (e.g. Bengtson and Cameron, 2004; Blix and Nordøy, 2007).

(iii) Transect placement and extrapolation from sampled to unsampled areas. An ideal survey design would have multiple randomly or regularly spaced transects extending in a north–south direction from the Antarctic continent to the ice edge to allow application of design-based inference methods for extrapolating densities estimated for the sampled transects to the entire region. Clearly this ideal design was not achieved in the shipboard sighting surveys in the Weddell Sea (Figure 2), and while aerial sighting surveys aspired to this design, the range of helicopters was insufficient to cover the full extent of ice, leaving the interior ice largely unsampled. With very limited sampling of the interior ice (some aerial photographic transects were flown), the estimates of abundance there were largely based on untested assumptions about seal distribution across the ice gradient. Estimates of Weddell seal abundance would be particularly prone to bias because their favoured fast-ice habitat received very little sampling. The magnitude, and even the direction, of bias relating to this issue is unclear.

(iv) Uncertainty or precision. Large-scale surveys of wildlife abundance often have low precision (= high uncertainty). None of the regional or circumpolar estimates derived from the Erickson surveys and listed in Table 1 were qualified with estimates of uncertainty or precision.

(v) Availability. One potential source of bias noted by Erickson and Hanson (1990) is the lack of accounting for seals in ice-free areas of the

Southern Ocean. As seals that do not haul out on the pack-ice, they are completely unavailable to estimation with the methods applied in the Erickson surveys, some alternate method would be needed to assess their status and importance.

Most of the above comments for the Erickson surveys apply to the Ross Sea surveys. The stratified analysis used by Ainley (1985) to estimate abundance should have minimised any bias that could otherwise have resulted from non-representative sampling.

Improved coordination of the APIS survey efforts and the application of state-of-the-art survey and analytical methods should have reduced many of the biases associated with the Erickson surveys and arguably provided a more realistic assessment of the uncertainty surrounding abundance estimates. Nevertheless, some biases are still likely to be inherent in estimates derived from the APIS surveys. The main bias that remains unresolved concerns the availability of seals to conventional survey methods that involve counting and capture. Southwell et al. (2008c) considered that this problem was likely to be greatest for leopard seals and least for crabeater seals, and recent studies of haul-out patterns and movement using satellite-linked dive recorders (e.g. Blix and Nordøy, 2007; Nordøy and Blix, 2009) highlight the importance of this concern for both Ross and leopard seals. Abundance estimates for these species could be significantly negatively biased because a large proportion of the population is pelagic for much of the time and hence not available for estimation.

Trends in abundance

It is difficult to reliably estimate population trends from the abundance estimates reported by the various surveys for several reasons. Firstly, very few repeat surveys have been undertaken in the same or similar regions. Secondly, a reanalysis of all data from previous surveys would be needed to make estimates of abundance from those surveys comparable with recent surveys from which abundance was estimated with newer analytical methods. This might not be possible if the original data from early surveys are not now available. Even if the original data were available, a reanalysis might not provide comparable results because the covariate data required to estimate and correct for detectability (e.g. distance data) were not recorded in most of the early surveys (this would be especially important for aerial sighting data). Finally, recent analyses have shown that uncertainty about abundance estimates is substantial, and this will make detection of anything but relatively large changes difficult.

Distribution and habitat use

As discussed above, sighting surveys to estimate abundance have capitalised on the dependence of Antarctic phocid seals on sea-ice as a substrate to haul out on to breed and moult in the late spring and summer months. Much of the available data and interpretations of distribution and habitat use of seals are based on observations made during those population surveys. Consequently, there has been a bias towards the use of haul-out habitat. The relatively recent development of satellite-linked dive recorders has allowed data on both haul-out and foraging habitat (both geographical and vertical) to be collected, and consequently, knowledge of habitat use has been increasing (summarised below).

Species reviews

Crabeater seals

Most satellite telemetry studies have found that crabeater seals are largely confined to the pack-ice (Bengtson et al., 1993; Nordøy et al., 1995; Burns et al., 2004). In the longest study through winter, Nordøy et al. (1995) noted that the only crabeater seal that left the pack-ice crossed a large bay of open water in about three days and then settled in the outer pack on the other side. Wall et al. (2007) found that association with pack-ice was not complete however, as seals spent around 14% of their time in open water after the breeding season. Satellite telemetry studies have also shown that when crabeater seals do haul out during spring and summer, they are mostly hauled out around solar midday (Bengtson and Cameron, 2004; Southwell, 2005), indicating that sighting surveys of hauled-out crabeater seals can provide reasonably unbiased broad inferences on both haul-out and foraging habitats at these times of year. In spring, when crabeater seals are breeding, shipboard surveys have found that breeding crabeater seals in East Antarctica were most likely to be present in a zone between the continental shelf break in the south and extending northward about 1.5 to 5° latitude, while non-breeders ranged further north (Southwell et al., 2005). Those areas are coincident with the known distribution of the crabeater seals' primary food source (Antarctic krill (*Euphausia superba*)), and also coincide with oceanographic fronts (e.g. the Antarctic Slope Front and the southern boundary of the Antarctic Circumpolar Current) which are thought to be areas of enhanced primary and secondary productivity. Ainley (1985) and Ackley et al. (2003) also reported greater densities of crabeater seals near the continental shelf break and the Antarctic Slope Front during early summer.

The retreating ice edge is also thought to be a zone of enhanced productivity in summer, but evidence of crabeater seals preferentially using the ice edge is equivocal. For example, Gilbert and Erickson (1977) and Laws (1984) reported that densities of crabeater seals were greater near the ice edge than farther south, whereas van Franeker (1992), Bester et al. (1995, 2002) and Flores et al. (2008) did not find any differences.

Some studies suggest that crabeater seals prefer ice floes of particular sizes, concentrations or thicknesses to haul out on (Condy, 1977; Bester et al., 2002; McMahon et al., 2002; Flores et al., 2008), whereas other studies found no evidence for preferences (Bester et al., 1995). Burns et al. (2004) concluded that the use of particular types of sea-ice habitat by crabeater seals along the Antarctic Peninsula in winter reflected the interaction between the reliance of seals on regions of high zooplankton abundance (e.g. near the bottom, at water mass boundaries, over varied topography, and perhaps under stable sea-ice) and their need to access air to breath and ice to rest. Based on shipboard surveys undertaken in the northeastern Weddell Sea pack-ice in winter, Plötz et al. (1991b) reported that crabeater seals were more abundant near the submarine Maud Rise (about 700 km north of the continental margin) than in other areas where ice coverage was more substantial. The distribution pattern of crabeater seals and other krill predators during those surveys coincided with the course of a warm water belt upwelling near Maud Rise. That upwelling evidently caused surface ice to melt, which then might have resulted in the release of large amounts of sea-ice algae and nutrients, and subsequently in large concentrations of krill, beneath the new sea-ice in winter.

The diving behaviour of crabeater seals has been examined in most areas of the Southern Ocean from summer to winter (Table 4), including the Weddell Sea (Bengtson and Stewart, 1992), Queen Maud Land (Nordøy et al., 1995), the Antarctic Peninsula (Burns et al., 2004, 2008), the Ross Sea (Ackley et al., 2003) and East Antarctica (Gales et al., 2004; Wall et al., 2007). The mean dive depth by crabeater seals in these studies ranged from 40 to 140 m, but dives as deep as 713 m have been recorded (Burns et al., 2004). Diving patterns vary seasonally, with a clear preference for diving during darkness and hauling out during daylight during summer and autumn and a reverse pattern in winter. Nordøy et al. (1995) reported that seals made deeper dives in February and shallower dives in June, whereas Hofmann et al. (2002) noted deepest dives occurring in May and shallowest dives in September. Most studies have reported diurnal or diel patterns in the diving behaviour of crabeater seals, perhaps in response to diel vertical migrations of prey.

Ross seals

In contrast to crabeater seals, Ross seals have been found to make long foraging trips north of the pack-ice into pelagic areas of the Southern Ocean for most of the year and return to the pack-ice only for short periods to breed and moult (Blix and Nordøy, 2007). This finding has changed the dogmatic view of Ross seal habitat use, which had previously concluded, based on sparse observations from sighting surveys, that Ross seals prefer dense concentrations of interior pack-ice (Wilson, 1975; Condy, 1976; Gilbert and Erickson, 1977). Clearly, for this species sighting surveys provide a very biased view of overall habitat use.

Satellite telemetry studies have shown that Ross seals forage to greater depths than crabeater seals, commonly diving to depths of 100–300 m and occasionally reaching depths of close to 800 m (Bengston and Stewart, 1997; Southwell, 2005; Blix and Nordøy, 2007) (Table 4).

Leopard seals

Satellite telemetry is also starting to shape a more complete view of leopard seal habitat use. Sighting surveys have provided few insights into leopard seal habitat use because very few sightings have ever been obtained from sighting surveys, and as for Ross seals, the potential for biased interpretation of sighting data exists if they spend long periods in the water and consequently are difficult to observe. Nordøy and Blix (2009) monitored two leopard seals from summer to winter near Queen Maud Land. The seals moved north as the pack-ice expanded and one eventually passed by the South Shetland Islands to as far north as 57°S, where it stayed in open water for a considerable time before moving south back to the ice edge. Northward movement of this scale is consistent with numerous observations over the last century of leopard seals hauling out at sub-Antarctic islands in winter, and year-round on some islands in close proximity to the south of the Antarctic Polar Front such as at South Georgia (Jessopp et al., 2004), Îles Kerguelen (Bester and Roux, 1986) and Heard Island (Gwynn, 1953). In contrast, Rogers et al. (2005) reported that leopard seals tagged at the fast-ice edge in Prydz Bay remained close to their tagging site with no evidence of pronounced north–south movement. While these studies are significant advances, our understanding of leopard seal habitat use is still limited and further study is required.

Satellite telemetry studies have reported that leopard seals are primarily shallow divers, with most dives to depths of 10–50 m and only occasionally as deep as, or deeper than, 200 m (Kuhn et al., 2006; Nordøy and Blix, 2009).

Weddell seals

Satellite telemetry studies and sighting surveys have suggested that Weddell seals primarily use fast-ice and nearby pack-ice habitats close to the coast. Testa (1994) found adult Weddell seals were reluctant to leave the fast-ice in McMurdo Sound where they had bred until March or April and then mostly remained within 50–100 km of their summer breeding colonies, although some seals moved longer distances and spent long periods in heavy winter pack-ice. Burns et al. (1999) found that Weddell seal pups from the McMurdo region travelled along the Antarctic continental coastline into pack-ice after leaving their natal area, but preferred to remain closer to the coast than adults. Lake et al. (2006) inferred from satellite telemetry studies that Weddell seals in East Antarctica foraged offshore within pack-ice in winter for periods of up to 30 days, but returned to the stable fast-ice to haul out. Observations of Weddell seals during shipboard sighting surveys in the pack-ice occur but are uncommon compared with the other species.

Weddell seal diving behaviour has been well studied (Table 4), reflecting the relative ease of access to this species for study when hauled out on fast-ice in several areas. They dive deeply, feeding primarily in the mid-water regions of the water column at depths of around 100–300 m. Some authors suggest that Weddell seals exhibit diurnal feeding patterns within two depth layers (0–160 m and 340–450 m) as a response to vertically migrating prey. Much effort has been devoted to classifying dives into behavioural classes such as pelagic foraging, benthic foraging, exploration and travelling using multivariate statistics. Between three and nine dive types have been classified depending on the method and type of data collected. Recent advances in dive-depth recording technology and the inclusion of cameras to record prey capture have also allowed the three-dimensional diving behaviour and presence of prey within the water column to be examined (e.g. Fuiman et al., 2007).

Diet

Methods used to measure or infer the diet of ice-breeding seals have included examination of stomach contents or faeces (scats), stable isotope analysis and indirect inference from studies of diving behaviour and habitat use.

Species reviews

Crabeater seal

Quantitative information on crabeater seal diet is available from analyses of stomach contents (Øritsland, 1977; Bengston, 1982; Lowry et al., 1988; Dzhamanov, 1990) and faeces (Green and Williams, 1986; Burns et al., 2004, 2008). Indirect inferences about diet have been made from morphology of teeth and mandibles (King, 1961), from observations of captive individuals (Klages and Cockcroft, 1990) and from data on seal movements and diving behaviour (Nordøy et al., 1995; Burns et al., 2004, 2008). Crabeater seals are believed to feed primarily on Antarctic krill (>90%), but also evidently eat fish and cephalopods when krill is not available (Øritsland, 1977). The information currently available is insufficient to assess geographic or temporal variability in diet.

Ross seal

Diet of Ross seals has been determined by analysis of stomach contents (King, 1969; Øritsland, 1977; Dzhamanov, 1990; Skinner and Klages, 1994) and ratios of stable isotopes in tissues (Rau et al., 1992). Diet has also been inferred from patterns of movement and diving behaviour (Bengtson and Stewart, 1997; Southwell, 2005; Blix and Nordøy, 2007). Those data indicate that Ross seals mostly eat squid (Moroteuthidae, Onychoteuthidae, Oegopsidae; ~60%) and fish (e.g. Myctophidae, Bathydraconidae; ~20% of the diet), and occasionally crustaceans (~10%) and benthic invertebrates (<10%) (Øritsland, 1977). There have been no studies of Ross seal diet in the Pacific or Indian sectors. There are insufficient data to assess geographic or temporal variability.

Leopard seal

Quantitative information on leopard seal diet is available from examination of stomach contents (Øritsland, 1977; Stone and Meier, 1981; Siniff and Stone, 1985; Dzhamanov, 1990), faeces (Øritsland, 1977; Green and Williams, 1986; Lowry et al., 1988; Walker et al., 1998; Hall-Apsland and Rogers, 2004; Casaux et al., 2009), direct observations of predatory behaviour (Hunt, 1973; Bester and Roux, 1986; Borsa, 1990; Kooyman et al., 1990), and inferences have been made from data on movement and diving behaviour (Kuhn et al., 2006; Nordøy and Blix, 2009). Those data indicate that leopard seals eat a variety of prey including fish, cephalopods, crustaceans, penguins and other seals (e.g. Green and Williams, 1986; Costa and Crocker, 1996), and that diet composition varies between seasons and regions. Green and Williams (1986) reported that fish (*Pleuragramma antarcticum*), followed by demersal species, were primary prey in winter and spring. Newly weaned crabeater seals appear to be important prey in December and January (Siniff and Stone, 1985; Siniff, 1991), and penguins are the primary prey in late January and February (Siniff and Stone, 1985), although analyses of scats and stomach contents from Prydz Bay in East Antarctica suggested that Adélie penguins (*Pygoscelis adeliae*) were eaten throughout the year at some locations (Rogers and Bryden, 1995; Hall-Apsland and Rogers, 2004). Krill is believed to be the most important prey in winter (Lowry et al., 1988; Siniff and Stone, 1985; Nordøy and Blix, 2009). In some areas (e.g. sub-Antarctic islands; Walker et al., 1998), Antarctic fur seals and penguins are important prey (Forcada et al., 2009) though rare sightings suggest that opportunistic prey can be variable (Edwards et al., 2009).

Weddell seal

Quantitative data on Weddell seal diet have been obtained from analyses of stomach contents (Øritsland, 1977; Weiner et al., 1981; Plötz, 1986, Plötz et al., 1991a), scats (Øritsland, 1977; Green and Burton, 1987; Burns et al., 1998, Casaux et al., 1997, 2006) and ratios of stable isotopes (Burns et al., 1998), and indirect inferences made from three-dimensional movements and diving patterns (Testa et al., 1989; Testa, 1994; Schreer and Testa, 1996; Plötz et al., 2001; Sato et al., 2002; Hindell et al., 2002; Davis et al., 2003; Watanabe et al., 2003; Fuiman et al., 2007). Most studies report that fish (mainly *P. antarcticum*) are the primary prey, followed by cephalopods and crustaceans, although there appears to be substantial geographic variability: for example, benthic fish, pelagic fish and crustaceans dominated the diet at the Vestfold Hills in East Antarctica (Green and Burton, 1987; Green et al., 1995), whereas pelagic fish dominated at McMurdo Sound (Burns et al., 1998), and cephalopods were the main prey at the South Shetland Islands and near Mawson (Lipinski and Woyciechowski, 1981; Clarke and McLeod, 1982; Green and Burton, 1987; Casaux et al., 1997). Studies have also found considerable variability within areas and seasons (Table 5).

Potential biases and uncertainties in diet data

Each of the diet methods has some potential biases and limitations. Analysis of stomach contents and scats can provide detailed quantitative, taxonomic dietary information, but the recovered remains of prey are generally only from the most recent meals. Differential rates of digestion of different prey can also result in biases toward prey with robust hard parts that can be identified. Stable isotopes in seal tissues can be used to infer general diets of seals over longer time periods (e.g. over several years for bone collagen), but fine-scale taxonomic detail is not possible. Inferring diet from diving behaviour and habitat use is indirect and circumstantial.

Diet studies are often based on small sample sizes (numbers of animals) leading to questions of how representative the samples are to the broader population. The patchy nature of diet data in both space and time, and the limited number of diet studies, also makes it difficult to make broader generalisations beyond the individual studies with any certainty, such as whether or how diet changes regionally, seasonally, or over the long term. Distilling these broad generalisations from the detailed diet studies, and attributing some level of certainty to them, are necessary and challenging steps before the available data can be incorporated into food-web models.

Concluding remarks

The data reviewed here are critical initial blocks for building food-web models. With regard to abundance, the relatively recent APIS surveys provide the best regional-scale estimates of abundance possible with existing methods. Past trends in abundance cannot be estimated with any confidence because of biases and differences in earlier methodology. Repeating the APIS surveys in the future may allow estimation of future trends, but the power to assess change would not be high, only large changes might be detected, and future surveys on the scale of APIS would be expensive. Knowledge of three-dimensional foraging habitat use is currently sufficient for characterisation at a very broad level (e.g. ice-dependent/independent, shelf/slope, shallow/deep), which may be sufficient for food-web modelling over large scales. Further knowledge of habitat use that would benefit food-web modelling is most likely to come from satellite telemetry work, especially on leopard and Ross seals, in regions and seasons where few data currently exist. Diet studies are not yet sufficient to characterise temporal or regional variation to inform spatially explicit food-web models, and this deficiency is a major constraint for food-web modelling.

Finally, food-web models are validated by or fitted to estimates of food consumption by the various ecosystem components. While abundance and diet are primary inputs to estimating food consumption, energetics models are needed to synthesise these with additional physiological and life-history parameters. A priority for future work should be the development of energetics models for ice-breeding seals so that the data reviewed here can be used to estimate food consumption and ultimately used to facilitate the building of food-web models.

Acknowledgements

We thank David Smith from the Australian Antarctic Division for producing the maps.

References

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

Ainley, D.G. 1985. Biomass of birds and mammals in the Ross Sea. In: Siegfried, W.R., P.R. Condy and R.M. Laws (Eds). *Antarctic Nutrient Cycles and Food Webs*. Springer-Verlag, Berlin: 498–515.

Bengtson, J.L. 1982. Reproductive ecology of crabeater and leopard seals along the Antarctic Peninsula. *Antarct. J. US*, 17: p. 185.

Bengtson, J.L. and B.S. Stewart. 1992. Diving and haul-out behavior of crabeater seals in the Weddell Sea, Antarctica, during March 1986. *Polar Biol.*, 12: 635–644.

Bengtson, J.L. and B.S. Stewart. 1997. Diving patterns of a Ross seal (*Ommatophoca rossii*) near the eastern coast of the Antarctic peninsula. *Polar Biol.*, 18: 214–218.

Bengtson, J.L. and M.F. Cameron. 2004. Seasonal haul-out patterns of crabeater seals (*Lobodon carcinophaga*). *Polar Biol.*, 27: 344–349.

Bengtson, J.L., R.D. Hill and S.E. Hill. 1993. Using satellite telemetry to study the ecology and behavior of Antarctic seals. *Kor. J. Polar Res.*, 4: 109–115.

Bengtson, J.L., J.L. Laake, P. Boveng, M.F. Cameron and B.S. Stewart. 2011. Distribution and abundance of Weddell, Ross, crabeater, and leopard seals in the Amundsen and Ross Seas, Antarctica. *Deep Sea Res.,* 58: 1261–1276.

Bester, M.N. and J.-P. Roux. 1986. Summer presence of leopard seals *Hydrurga leptonyx* at the Courbet Peninsula, Iles Kerguelen. *S. Afr. J. Antarct. Res.*, 16: 29–32.

Bester, M.N. and P.N. Odendaal. 2000. Abundance and distribution of Antarctic pack ice seals in the Weddell Sea. In: Davison, W., C. Howard-Williams and P. Broady (Eds). *Antarctic Ecosystems: Models for Wider Ecological Understanding*. Caxton Press, Christchurch: 51–55.

Bester, M.N., A.W. Erickson and W.H. Ferguson. 1995. Seasonal change in the distribution and density of seals in the pack ice off Princess Martha Coast, Antarctica. *Ant. Sci.*, 7: 357–364.

Bester, M.N., J.W.H. Ferguson and F.C. Jonker. 2002. Population densities of pack ice seals in the Lasarev Sea, Antarctica. *Ant. Sci.*, 14: 123–127.

Blix, A.S. and E.S. Nordøy. 2007. Ross seal (*Ommatophoca rossii*) annual distribution, diving behaviour, breeding and moulting, off Queen Maud Land, Antarctica. *Polar Biol.*, 30: 1449–1458.

Borsa, P. 1990. Seasonal occurrence of the leopard seal (*Hydrurga leptonyx*) in the Kerguelen Islands. *Can. J. Zool.*, 68: 405–408.

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

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

Burns, J.M., D.P. Costa, M.A. Fedak, M.A. Hindell, C.J.A. Bradshaw, N.J. Gales, B. McDonald, S.J. Trumble and D.E. Crocker. 2004. Winter habitat use and foraging behavior of crabeater seals along the Western Antarctic Peninsula. *Deep-Sea Res. II*, 51: 2279–2303.

Burns, J.M., M.A. Hindell, C.J.A. Bradshaw and D.P. Costa. 2008. Fine-scale habitat selection of crabeater seals as determined by diving behavior. *Deep Sea Res. II*, 55: 500–514.

Casaux, R., A. Baroni and A. Carlini. 1997. The diet of the Weddell seal *Leptonychotes weddelli* at Harmony Point, South Shetland Islands. *Polar Biol.*, 18: 371–375.

Casaux, R., A. Baroni and A. Ramon. 2006. The diet of the Weddell Seal *Leptonychotes weddellii* at the Danco Coast, Antarctic Peninsula. *Polar Biol.*, 29: 257–262.

Casaux, R., A. Baroni, A. Ramón, A. Carlini, M. Bertolin and C.Y. DiPrinzio. 2009. Diet of the leopard seal *Hydrurga leptonyx* at the Danco Coast, Antarctic Peninsula. *Polar Biol.*, 32: 307–310.

Clarke, M.R. and M. McLeod. 1982. Cephalopod remains in the stomachs of eight Weddell seals. *Br. Antarct. Surv. Sci. Rep.*, 57: 33–40.

Condy, P.R. 1976. Results of the third seal survey in the King Haakon VII Sea, Antarctica. *S. Afr. J. Antarct. Res.*, 6: 2–8.

Condy, P.R. 1977. Results of the fourth seal survey in the King Haakon VII Sea, Antarctica. *S. Afr. J. Antarct. Res.*, 7: 10–13.

Costa, D.P. and D.E. Crocker. 1996. Marine Mammals of the Southern Ocean. Foundations for Ecological Research West of the Antarctic Peninsula. *Antarct. Res. Ser.*, 70: 287–301.

Davis, R.W., M. Castellini, M. Horning, M. Davis and G. Kooyman. 1982. Winter ecology of Weddell seals at White Island. *Antarct. J. US*, 17: 183–184.

Davis, R.W., L.A. Fuiman, T.M. Williams, M. Horning and W. Hagey. 2003. Classification of Weddell seal dives based on 3-dimensional movements and video-recorded observations. *Mar. Ecol. Prog. Ser.*, 263: 109–122.

Dearborn, J.H. 1965. Food of Weddell seals at McMurdo Sound, Antarctica. *J. Mammal.*, 46: 37–43.

Dzhamanov, G.K. 1990. Some aspects of the biology and distribution of ice-inhabiting seals near the Balleny Islands and east of the d'Urville Sea in 1986–87. *Morskie Mlekopitayushchie*, 112–129.

Edwards, E.W.J., J. Forcada and G.T. Crossin. 2009. First documentation of leopard seal predation of South Georgia pintail duck. *Polar Biol.*, 33: 403–405.

Eklund, C.R. 1964. Population studies of Antarctic seals and birds. In: Carrick, R., M. Holdgate and J. Prevost (Eds). *Biologie Antarctique*. Hermann, Paris: 415–419.

Eklund, C.R. and E.L. Atwood. 1962. A population study of Antarctic seals. *J. Mammal.*, 43: 229–238.

Erickson, A.W. 1984. Aerial census of seals, whales and penguins in the pack ice of the northwestern Weddell Sea, November 1983. *Antarct. J. US*, 19: 121–124.

Erickson, A.W. and M.B. Hanson. 1990. Continental estimates and population trends of Antarctic seals. In: Kerry, K.R. and G. Hempel (Eds). *Antarctic Ecosystems: Ecological Change and Conservation.* Springer-Verlag, Berlin: 253–264.

Erickson, A.W., D.R. Cline and R.J. Hoffman. 1969. Population study of seals in the Weddell Sea. *Antarct. J. US*, 4: 99–100.

Erickson, A.W., R.J. Hofman, R.J. Oehlenschlager, J. Otis and D. Kuehn. 1971. Seal population studies in the Ross Sea. *Antarct. J. US*, 6: 98–99.

Erickson, J.R., J.R. Gilbert, G.A. Petrides, R.J. Oehlenschlager, A.A. Sinha and J. Otis. 1972. Populations of seals, whales, and birds in the Bellinghausen and Amundsen Seas. *Antarct. J. US*, 6: 98–99.

Erickson, A.W., J.R. Gilbert and J. Otis. 1973. Census of pelagic seals off the Oates and George V coasts, Antarctica. *Antarct. J. US*, 8: 191–194.

Erickson, A.W., R.N. Denney, J.J. Brueggeman, A.A. Sinha, M.M. Bryden and J. Otis. 1974. Seal and bird populations off Adelie, Claire, and Banzare coasts. *Antarct. J. US*, 9: 292–296.

Erickson, A.W., M.B. Hanson and D.M. Kehoe. 1983. Population densities of seals and whales observed during the 1983 circumnavigation of Antarctica by the USCGC Polar Star. *Antarct. J. US*, 18: 163–166.

Erickson, A.W., L.J. Bledsoe and M.B. Hanson. 1989. Bootstrap correction for diurnal activity cycle in census data for Antarctic seals. *Mar. Mammal Sci.*, 5: 29–56.

Flores, H., C. Haas, J.A. van Franeker and E. Meesters. 2008. Density of pack-ice seals and penguins in the western Weddell Sea in relation to ice thickness and ocean depth. *Deep Sea Res. II*, 55: 1068–1074.

Forcada, J. and P.N. Trathan. 2008. Abundance estimates for crabeater, Weddell and leopard seals at the Antarctic Peninsula and in the western Weddell Sea (90°–30°W, 60°–80°S). Document WG-EMM-PSW-08/6. CCAMLR, Hobart, Australia: 9 pp.

Forcada, J., D. Malone, J.A. Royle and I.J. Staniland. 2009. Modelling predation by transient leopard seals for an ecosystem-based management of Southern Ocean fisheries. *Ecol. Model.*, 220: 1513–1521.

Fuiman, L.A., R.W. Davis and T.M. Williams. 2002. Behavior of midwater fishes under the Antarctic ice: observations by a predator. *Mar. Biol.*, 140: 815–822.

Fuiman, L.A., K.M. Madden, T.M. Williams and R.W. Davis. 2007. Structure of foraging dives by Weddell seals at an offshore isolated hole in the Antarctic fast-ice environment. *Deep Sea Res. II*, 54: 270–289.

Gales, N.J., W.R. Fraser, D.P. Costa and C. Southwell. 2004. Do crabeater seals forage cooperatively? *Deep-Sea Res. II*, 51: 2305–2310.

Gilbert, J.R. and A.W. Erickson. 1977. Distribution and abundance of seals in the pack ice of the Pacific sector of the Southern Ocean. In: Llano, L. (Ed.). *Adaptations within Antarctic Ecosystems*. Smithsonian Institute, Washington DC: 703–740.

Green, K. and R. Williams. 1986. Observations on food remains in faeces of elephant, leopard and crabeater seals. *Polar Biol.*, 6: 43–45.

Green, K. and H.R. Burton. 1987. Seasonal and geographical variation in the food of Weddell seals, *Leptonychotes weddellii*, in Antarctica. *Aust. Wildl. Res.*, 14: 475–489.

Green, K., H.R. Burton and D.J. Watts. 1995. Studies of the Weddell seal in the Vestfold Hills, East Antarctica. *ANARE Res. Notes*, 93: 64 pp.

Gwynn, A.M. 1953. The status of the leopard seal at Heard Island and Macquarie Island, 1948–1950. *ANARE Research Expedition Interim Report No. 3*. Antarctic Division, Department of External Affairs, Melbourne: 33 pp.

Hall-Apsland, S.A. and T.L. Rogers. 2004. Summer diet of leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Eastern Antarctica. *Polar Biol.*, 27: 729–734.

Harcourt, R.G., M.A. Hindell, D.G. Bell and J.R. Waas. 2000. Three-dimensional dive profiles of free-ranging Weddell seals. *Polar Biol.*, 23: 479–487.

Hindell, M.A., R. Harcourt, J.R. Waas and D. Thompson. 2002. Fine-scale three-dimensional spatial use by diving, lactating female Weddell seals *Leptonychotes weddellii*. *Mar. Ecol. Prog. Ser.*, 242: 275–284.

Hofmann E.E., J.M. Klinck, D.P. Costa, K.L. Daly, J.J. Torres and W.R. Fraser. 2002. U.S. Southern Ocean Global Ecosystems Dynamics Program. *Oceanography*, 15: 64–74.

Hunt, J.F. 1973. Observations on the seals of Elephant Island, South Shetland Islands, 1970–71. *Br. Antarct. Surv. Sci. Rep.*, 36: 99–104.

Jessopp, M.J., J. Forcada, K. Reid, P.N. Trathan, and E.J. Murphy. 2004. Winter dispersal of leopard seals (*Hydrurga leptonix*) environmental factors influencing demographics and seasonal abundance. *J. Zool.*, 263: 251–258.

King, J.E. 1961. The feeding mechanism and jaws of the crabeater seal. *Mammalia*, 25: 462–466.

King, J.E. 1969. Some aspects of the anatomy of the Ross seal *Ommatophoca rossii* (Pinnipedia: Phocidae). *Br. Antarct. Surv. Sci. Rep.*, 63: 1–54.

Klages, N.T.W. and V.G. Cockcroft. 1990. Feeding behaviour of a captive crabeater seal. *Polar Biol.*, 10: 403–404.

Kooyman, G.L., D. Croll, S. Stone and S. Smith. 1990. Emperor penguin colony at Cape Washington, Antarctica. *Polar Rec.*, 26: 103–108.

Kuhn, C.E., B.I. McDonald, S.A. Shaffer, J. Barnes, D.E. Crocker, J. Burns and D.P. Costa. 2006. Diving physiology and winter foraging behavior of a juvenile leopard seal (*Hydrurga leptonyx*). *Polar Biol.*, 29: 303–307.

Lake, S., H. Burton and J. van den Hoff. 2003. Regional, temporal and fine-scale spatial variation in Weddell seal diet at four coastal locations in east Antarctica. *Mar. Ecol. Prog. Ser.*, 254: 293–305.

Lake, S.E., H. Burton and S. Wotherspoon. 2006. Movements of adult female Weddell seals during the winter months. *Polar Biol.*, 29: 270–279.

Laws, R.M. 1953. The seals of the Falkland Islands and dependencies. *Oryx*, 2: 87–97.

Laws, R.M. 1984. Seals. In: Laws, R.M. (Ed.). *Antarctic Ecology*. Vol. 2. Academic Press, London: 621–715.

Lipinski, M. and M. Woyciechowski. 1981. Cephalopods in the food of Weddell seals from the Admiralty Bay (King George Island, South Shetland Islands). *Polish Polar Res.*. 2: 163–167.

Lowry, L.F., J.W. Testa and W. Calvert. 1988. Notes on winter feeding of crabeater and leopard seals near the Antarctic Peninsula. *Polar Biol.*, 8: 475–478.

McMahon, C., M. Hindell, T. Dorr and R.A. Massom. 2002. Winter distribution and abundance of crabeater seals off George V Land, East Antarctica. *Antarct. Sci.*, 14: 128–133.

Mitani, Y., K. Sato, S. Ito, M.F. Cameron, D.B. Siniff and Y. Naito. 2003. A method for reconstructing three-dimensional dive profiles of marine mammals using geomagnetic intensity data: results from two lactating Weddell seals. *Polar Biol.*, 26: 311–317.

Mitani, Y., Y. Watanabe, K. Sato, M.F. Cameron and Y. Naito. 2004. 3D diving behavior of Weddell seals with respect to prey accessibility and abundance. *Mar. Ecol. Prog. Ser.*, 281: 275–281.

Nordøy, E.S. and A.S. Blix. 2009. Movements and dive behaviour of two leopard seals (*Hydrurga leptonix*) off Queen Maud Land, Antarctica. *Polar Biol.*, 32: 263–270.

Nordøy, E.S., L. Folkow and A.S. Blix. 1995. Distribution and diving behaviour of crabeater seals (*Lobodon carcinophagus*) off Queen Maud Land. *Polar Biol.*, 15: 261–268.

Øritsland, T. 1977. Food consumption of seals in the Antarctic pack ice. In: Llano, G.A. (Ed.). *Adaptations Within Antarctic Ecosystems*. Smithsonian Institute, Washington DC: 749–768.

Plötz, J. 1986. Summer diet of Weddell seals (*Leptonychotes weddelli*) in the eastern and southern Weddell Sea, Antarctica. *Polar Biol.*, 6: 97–102.

Plötz, J., W. Ekau and P.J.H. Reijnders. 1991a. Diet of Weddell seals Leptonychotes weddellii at Vestkapp, eastern Weddell Sea (Antarctica), in relation to local food supply. *Mar. Mammal Sci.*, 7: 136–144.

Plötz, J. , H. Weidel and M. Bersch. 1991b.Winter aggregations of marine mammals and birds in the north-eastern Weddell Sea pack ice, *Polar Biol.*, 11: 305–309.

Plötz, J., H. Bornemann, R. Knust, A. Schroder and M.N. Bester. 2001. Foraging behaviour of Weddell seals, and its ecological implications. *Polar Biol.*, 24: 901–909.

Plötz, J., D. Steinhage and H. Bornemann. 2011a. Seal census raw data during campaign EMAGE-I, doi:10.1594/PANGAEA.760097.

Plötz, J., D. Steinhage and H. Bornemann. 2011b. Seal census raw data during campaign EMAGE-II, doi:10.1594/PANGAEA.760098.

Plötz, J., D. Steinhage and H. Bornemann. 2011c. Seal census raw data during campaign EMAGE-III, doi:10.1594/PANGAEA.760099.

Plötz, J., D. Steinhage and H. Bornemann. 2011d. Seal census raw data during campaign EMAGE-IV, doi:10.1594/PANGAEA.760100.

Plötz, J., D. Steinhage and H. Bornemann. 2011e. Seal census raw data during campaign EMAGE-V, doi:10.1594/PANGAEA.760101.

Rau, G.H., D.G. Ainley, J.L. Bengtson, J.J. Torres and T.L. Hopkins. 1992. 15N/14N and 13C/12C in Weddell Sea birds, seals, and fish: implications for diet and trophic structure. *Mar. Ecol. Prog. Ser.*, 84: 1–8.

Rogers, T. and M.M. Bryden. 1995. Predation of Adelie penguins (*Pygoscelis adeliae*) by leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Antarctica. *Can. J. Zool.*, 73: 1001–1004.

Rogers, T.L., C.J. Hogg and A. Irvine. 2005. Spatial movement of adult leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Eastern Antarctica. *Polar Biol.*, 28: 456–463.

Sato, K., Y. Mitani, M.F. Cameron, D.B. Siniff, Y. Watanabe, and Y. Naito. 2002. Deep foraging dives in relation to the energy depletion of Weddell seal (*Leptonychotes weddellii*) mothers during lactation. *Polar Biol.*, 25: 696–702.

Scheffer, V.B. 1958. *Seals, Sea Lions and Walruses*: A Review of the Pinnipedia. Stanford University Press, California: 179 pp.

Schreer, J.F. and J.W. Testa. 1995. Statistical classification of diving behavior. *Mar. Mammal Sci.*, 11 (1): 85–93.

Schreer, J.F. and J.W. Testa. 1996. Classification of Weddell seal diving behavior. *Mar. Mammal Sci.*, 12: 227–250.

Siniff, D.B. 1991. An overview of the ecology of Antarctic seals. *Amer. Zool.*, 31: 143–149.

Siniff, D.B. and S. Stone. 1985. The role of the leopard seal in the tropho-dynamics of the Antarctic marine ecosystem. In: Siegfried, W.R., P.R. Condy and R.M. Laws (Eds). *Antarctic Nutrient Cycles and Food Webs*. Springer-Verlag: 555–559.

Siniff, D.B., D.R. Cline and A.W. Erickson. 1970. Population densities of seals in the Weddell Sea, Antarctica, in 1968. In: Holdgate, M.W. (Ed.). *Antarctic Ecology*. Academic Press, London: 377–394.

Skinner, J.D. and N.T.W. Klages. 1994. On some aspects of the biology of the Ross seal *Ommatophoca rossii* from King Haakon VII Sea, Antarctica. *Polar Biol.*, 14: 467–472.

Southwell, C. 2003. Haul-out behaviour of two Ross seals off eastern Antarctica. *Antarct. Sci.*, 15: 257–258.

Southwell, C. 2005. Optimising the timing of visual surveys of crabeater seal abundance: haulout behaviour as a consideration. *Wildl. Res.*, 32: 333–338.

Southwell, C.J., K.R. Kerry and P.H. Ensor. 2005. Predicting the distribution of crabeater seals off east Antarctica during the breeding season. *Mar. Ecol. Prog. Ser.*, 299: 297–309.

Southwell, C., C.G.M. Paxton, D. Borchers, P. Boveng, E.S. Nordøy and A.S. Blix. 2008a. Estimating population status under conditions of uncertainty: the Ross seal in east Antarctica. *Antarct. Sci.*, 20: 123–133.

Southwell, C., C.G.M. Paxton, D.L. Borchers, P. Boveng and W.K. de la Mare. 2008b. Taking account of dependent species in management of the Southern Ocean krill fishery: estimating crabeater seal abundance off east Antarctica. *J. Appl. Ecol.*, 45: 622–631.

Southwell, C., C.G.M. Paxton, T. Rogers, D.L. Borchers, P. Boveng and W.K. de la Mare. 2008c. Uncommon or cryptic? Challenges in estimating leopard seal abundance by conventional but state-of-the-art methods. *Deep Sea Res. I*, 55: 519–531.

Stone, S. and T. Meier. 1981. Summer leopard seal ecology along the Antarctic Peninsula. *Antarct. J. US*, 16: 151–152.

Testa, J.W. 1994. Over-winter movements and diving behaviour of female Weddell seals (*Leptonychotes weddelli*) in the southwestern Ross Sea, Antarctica. *Can. J. Zool.*, 72: 1700–1710.

Testa, J.W., S.E.B. Hill and D.B. Siniff. 1989. Diving behavior and maternal investment in Weddell seals (*Leptonychotes weddellii*). *Mar. Mammal Sci.*, 5: 399–405.

van Franeker, J.A. 1992. Top predators as indicators for ecosystem events in the confluence zone and marginal ice zone of the Weddell and Scotia Seas, Antarctica, November 1988 to January 1989 (EPOS Leg 2). *Polar Biol.*, 12: 93–102.

Walker, T.R., I.L. Boyd, D.J. McCafferty, N. Huin, R.I. Taylor, and K. Reid. 1998. Seasonal occurrence and diet of leopard seals (*Hydrurga leptonyx*) at Bird Island, South Georgia. *Antarct. Sci.*, 10: 75–81.

Wall, S.M., C.J.A. Bradshaw, C.J. Southwell, N.J. Gales and M.A. Hindell. 2007. Crabeater seal diving behaviour in eastern Antarctica. *Mar. Ecol. Prog. Ser.*, 337: 265–277.

Watanabe, Y., Y. Mitani, K. Sato, M.F. Cameron and Y. Naito. 2003. Dive depths of Weddell seals in relation to vertical prey distribution as estimated by image data. *Mar. Ecol. Prog. Ser.*, 252: 283–288.

Weiner, J., M. Woyciechowski and J. Zieliński. 1981. An attempt to determine the digestibility of natural food in Antarctic seals using tracer method: a preliminary study. *Pol. Polar Res.*, 2: 153–163.

Wilson, V.J. 1975. A second survey of seals in the King Haakon VII Sea, Antarctica. *S. Afr. J. Antarct. Res.*, 5: 31–36.

Table 1: Regional and circumpolar estimates of the population size of ice-breeding seals. Only those estimates from Erickson surveys identified in Erickson and Hanson (1990) as the most reliable are included. Estimates are rounded to the nearest 100. - Information not stated or estimate not provided in publication.

Survey	Region	Survey year(s)	Crabeater	Ross	Leopard	Weddell	Reference
Early surveys/ estimates	Falkland Is. Dep.	-	1 000 000	10 000	40 000	800 000	1
	Circumpolar	-	2 000 000–5 000 000	20 000–50 000	100 000–300 000		2
	Circumpolar	1956/57	4 962 000–8 081 000	51 400	152 500	200 000–500 000	3
Erickson surveys	60°W–20°W	1968/69 and 1969/70	8 246 800 and 10 597 500	2 500 and 10 200	38 300 and 82 400	211 800 and 46 900	4
	60°W–20°W	1968/69 and 1969/70	2 241 300 and 2 780 900	-	-	-	5
	20°W–20°E	1982/83	806 400	17 500	28 700	17 200	5
	20°W–10°E	1968/69–1972/73	1 686 000	-	-	-	6
	20°E–70°E	1968/69–1972/73	798 000	-	-	-	6
	20°E–90°E	1982/83	745 900	-	-	-	5
	90°E–160°E	1972/73–1973/74	938 900	-	68 000	69 200	5
	80°E–140°E	1968/69–1972/73	772 000	-	-	-	6
	145°E–170°E	1972/73	472 400	64 000	23 200	64 900	6, 7
	160°E–130°W	1971/72–1972/73	1 293 000	18 900	55 200	49 400	5
	135°W–80°W	1971/72	1 193 400	37 500	48 600	45 600	6, 7
	130°W–60°W	1971/72	632 700	23 700	61 400	38 400	5
	Circumpolar	1968/69–1969/70	50 000 000–75 000 000	-	-	-	4
	Circumpolar	1968/69–1972/73	≥15 000 000	220 000	220 000–440 000	800 000	6
	Circumpolar	1968/69–1982/83	≥7 000 000	131 400	296 500	799 000	5
Ross Sea surveys	170°E–160°W	1976/77–1979/80	203 700	5 100	8 000	32 000	8
APIS surveys	150°E–100°W	1999/00	1 736 000 (1 219 000–2 472 000)	22 600 (11 700–43 700)*	15 000 (3 500–65 000)	331 000 (144 000–759 000)*	9
	90°W–30°W	1998/99	3 187 000 1 754 000–4 748 000)	-	13 200 (3 700–23 100)	302 000 (77 000–576 000)	10
	64°E–150°E	1999/00	946 400 (726 400–1 396 700)	55 900 (27 700–187 500)	7 300 (3 700–14 500)	-	11
	26°W–7°W	1997/98	3 564 000**	-	-	-	12

[1] Laws (1953); [2] Scheffer (1958); [3] Eklund and Atwood (1962); [4] Erickson et al. (1971); [5] Erickson and Hanson (1990); [6] Laws (1984); [7] Gilbert and Erickson (1977); [8] Ainley (1985); [9] Bengtson et al. (2011); [10] Forcada and Trathan (2008); [11] Southwell et al. (2008a, 2008b, 2008c); [12] Bester and Odendaal (2000)

* These estimates cover a smaller geographic range than for crabeater and leopard seal estimates derived from this survey effort because sighting surveys were too late to construct reliable correction for haul-out (Ross seal) or didn't cover all fast-ice (Weddell seal)

** Preliminary analysis: authors consider estimates to be positively biased.

Table 2: Survey details relating to the estimation of density in sampled strips for shipboard surveys of ice-breeding seals. Methods for estimating on-ice density: PE – personal experience; ST – strip transect; LT – line transect; MRLT – mark-recapture line transect/method of correcting on-ice density for haul-out probability; O – from observational data; DL – from data logger; N – no correction. - Information not stated in publication.

Survey	Survey year(s)	Time of year (month)	Time of day (local hr)	Strip half-width (m)	Independent observers	Method for estimating density	References
Early surveys	1956/57	Dec–Jan	6–21	Unlimited	No	ST/N	1
'Erickson' surveys	1967/68	Feb–Mar	00–24	200	No	ST/O	2, 3
	1968/69	Jan–Mar	Daylight	201	No	ST/O	3, 4, 5
	1971/72	Jan–Feb	-	232	No	ST/O	6, 7
	1973/74	Jan–Feb	-	-	No	ST/O	3, 8
	1982/83	Jan–Mar	3–23	232	No	ST/O	3, 9
Ross Sea surveys	1976/77–1979/80	Dec–Jan	0–23	300	No	ST/O	10
APIS surveys	1999/00	Jan–Mar	4–18	Unlimited	No	LT/DL	11
	1999/00	Dec–Jan	8–18	Unlimited	Yes	MRLT/DL	12

[1] Eklund and Atwood (1962); [2] Siniff et al. (1970); [3] Erickson and Hanson (1990); [4] Erickson et al. (1969); [5] Erickson et al. (1971), [6] Erickson et al. (1972); [7] Gilbert and Erickson (1977); [8] Erickson et al. (1974); [9] Erickson et al. (1983); [10] Ainley (1985); [11] Bengtson et al. (2011); [12] Southwell et al. (2008a, 2008b, 2008c)

Table 3: Survey details relating to the estimation of density in sampled strips for aerial surveys of ice-breeding seals. Survey type: AP – aerial photographic survey; SS – sighting survey/method for estimating on-ice density: ST – strip transect; LT – line transect; MRLT – mark-recapture line transect/method of correcting on-ice density for haul-out probability: O – from observational data; DL – from data logger; N – no correction. - Information not stated.

Survey	Survey year(s)	Time of year (month)	Time of day (local hr)	Speed (knots)	Altitude (m)	Strip half-width (m)	Independent observers	Method for estimating density	References
'Erickson' surveys	1970/71	Nov	-	-	350	600	No	AP/ST/-	1
	1971/72	Jan–Feb	-	-	152	463	No	SS/ST/O	1, 2
	1971/72	Jan	-	-	350	600	No	AP/ST/O	1
	1972/73	Jan	11–14	-	152	463	No	SS/ST/O	1, 3
	1973/74	Jan–Feb	-	-	-	-	No	SS/ST/N	4
	1982/83	Jan–Feb	10–20	-	76	463	No	SS/ST/N	5
	1983/84	Nov	8–19	-	91	463	No	SS/ST/N	6
APIS surveys	1999/00	Jan–Mar	7–18	90	91	519	Yes	SS/LT/DL	7
	1998/99	Jan	-	-	-	Unlimited	Yes	SS/MRLT/DL	8
	1999/00	Dec–Jan	9–15	90	130	1000	Yes	SS/MRLT/DL	9
	1997/98	Jan–Mar	11–15	60	61	312	No	SS/ST/N	10
	1996/97	-	-	100	91	-	No	SS/LT/DL	11
	1996/01	Dec–Jan	10–18	240	152	35	No	AP/ST/DL	12

[1] Gilbert and Erickson (1977); [2] Erickson et al. (1972); [3] Erickson et al. (1973); [4] Erickson et al. (1974); [5] Erickson et al. (1983); [6] Erickson (1984); [7] Bengtson et al. (2011); [8] Forcada and Trathan (2008); [9] Southwell et al. (2008a, 2008b, 2008c); [10] Bester and Odendaal (2000); [11] Blix (pers. comm.); [12] Plötz et al. (pers. comm., 2011a to 2011e)

Table 4: Diving studies of crabeater, Ross, leopard and Weddell seals in three sectors of Antarctica in summer, autumn, spring and winter. The grey bars represent sectors and seasons where studies occurred; light grey represents diving depths of 0–100 m, dark grey > 100 m.

Species	Sector	Summer	Autumn	Winter	Spring	References
Crabeater	70°W–30°E					1, 2, 3, 4, 5
	30°E–150°E					6
	150°E–70°W					
Ross	70°W–30°E					7, 8
	30°E–150°E					9
	150°E–70°W					
Leopard	70°W–30°E					10, 11
	30°E–150°E					
	150°E–70°W					
Weddell	70°W–30°E					12
	30°E–150°E					13
	150°E–70°W					13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25

[1] Bengtson and Stewart (1992); [2] Hofmann et al. (2002); [3] Burns et al. (2004); [4] Burns et al. (2008); [5] Nordøy et al. (1995); [6] Wall et al. (2007); [7] Bengtson and Stewart (1997); [8] Blix and Nordøy (2007); [9] Southwell (2005); [10] Kuhn et al. (2006); [11] Nordøy and Blix (2009); [12] Plötz et al. (2001); [13] Sato et al. (2002); [14] Testa et al. (1989); [15] Schreer and Testa (1995); [16] Testa (1994); [17] Burns et al. (1999); [18] Harcourt et al. (2000); [19] Hindell et al. (2002); [20] Fuiman et al. (2002); [21] Davis et al. (2003); [22] Watanabe et al. (2003); [23] Mitani et al. (2003); [24] Mitani et al. (2004); [25] Fuiman et al. (2007).

Table 5: Proportion of fish, cephalopod, crustacean and (for the leopard seal) bird and seal prey found in the diet of ice-breeding seals in three sectors of Antarctica in summer, autumn, spring and winter obtained from analyses of scat (Sc), stomach contents (Sa), ratios of stable isotope in tissue (Is) and dive behaviour (D). Note × denotes the presence of a prey item where no proportion was given.

Species	Sector	Prey item	Summer	Autumn	Winter	Spring	References
Crabeater	70°W–30°E	Fish		×	3	3	1, 2, 3, 4, 5, 6
		Cephalopods			2	2	
		Crustaceans	×	×	94	94	
	30°E–150°E	Fish			×	×	7
		Cephalopods					
		Crustaceans					
	150°E–70°W	Fish					8
		Cephalopods					
		Crustaceans	×				
Ross	70°W–30°E	Fish	×	×	22	22	1, 9, 10, 11
		Cephalopods	×	×	64	64	
		Crustaceans			9	9	
	30°E–150°E	Fish					
		Cephalopods					
		Crustaceans					
	150°E–70°W	Fish					
		Cephalopods					
		Crustaceans					
Leopard	70°W–30°E	Fish	3	3	13	53	1, 3, 12, 13, 14, 15, 16, 17, 18
		Cephalopods	1	1	1–11	11	
		Crustaceans	83	83	37	1	
		Birds	13	13–46	35	35	
		Seals	×	53	53	×	
	30°E–150°E	Fish	34	34	×		7, 19, 20
		Cephalopods					
		Crustaceans	18	18	×		
		Birds	90	90			
		Seals	13	13			
	150°E–70°W	Fish					8, 21
		Cephalopods					
		Crustaceans	×	×			
		Birds	×	×			
		Seals					
Weddell	70°W–30°E	Fish	33–94	94	53	53–96	22, 23, 24, 25, 26, 27, 28
		Cephalopods	6–66	6	11	4–11	
		Crustaceans	1	×	1	1	
	30°E–150°E	Fish	16–77	16–77	16–77	16–77	29, 30
		Cephalopods	3–82	3–82	3–82	3–82	
		Crustaceans	1–20	1–20	1–20	1–20	
	150°E–70°W	Fish	62–97	62–99	62–97	62–97	29, 31, 32, 33, 34
		Cephalopods	1–4	1–4	1–4	1–4	
		Crustaceans	×	×	×	×	

[1] Øritsland (1977) (St, Sc); [2] Bengtson (1982) (St); [3] Lowry et al. (1988) (St); [4] Burns et al. (2004) (Sc, D); [5] Burns et al. (2008) (Sc, D); [6] Nordøy et al. (1995) (D); [7] Green and Williams (1986) (Sc); [8] Dzhamanov (1990) (St); [9] Bengtson and Stewart (1997) (D); [10] Skinner and Klages (1994) (St); [11] Blix and Nordøy (2007) (D); [12] Hunt (1973) (O); [13] Stone and Meier (1981) (St); [14] Siniff and Stone (1985) (St); [15] Walker et al. (1998) (Sc); [16] Kuhn et al. (2006) (D); [17] Casaux et al. (2009) (Sc); [18] Nordøy and Blix (2009) (D); [19] Bester and Roux (1986) (O); [20] Hall-Apsland and Rogers (2004) (Sc); [21] Kooyman et al. (1990) (O); [22] Weiner et al. (1981) (St); [23] Lipinski and Woyciechowski (1981) (St); [24] Clarke and McLeod (1982) (St); [25] Plötz (1986) (St); [26] Casaux et al. (1997) (Sc); [27] Casaux et al. (2006) (Sc); [28] Plötz et al. (1991a) (St); [29] Green and Burton (1987) (Sc); [30] Lake et al. (2003) (Sc); [31] Dearborn (1965) (St); [32] Davis et al. (1982) (St); [33] Testa (1994) (Sc); [34] Burns et al. (1998) (Sc, Is)

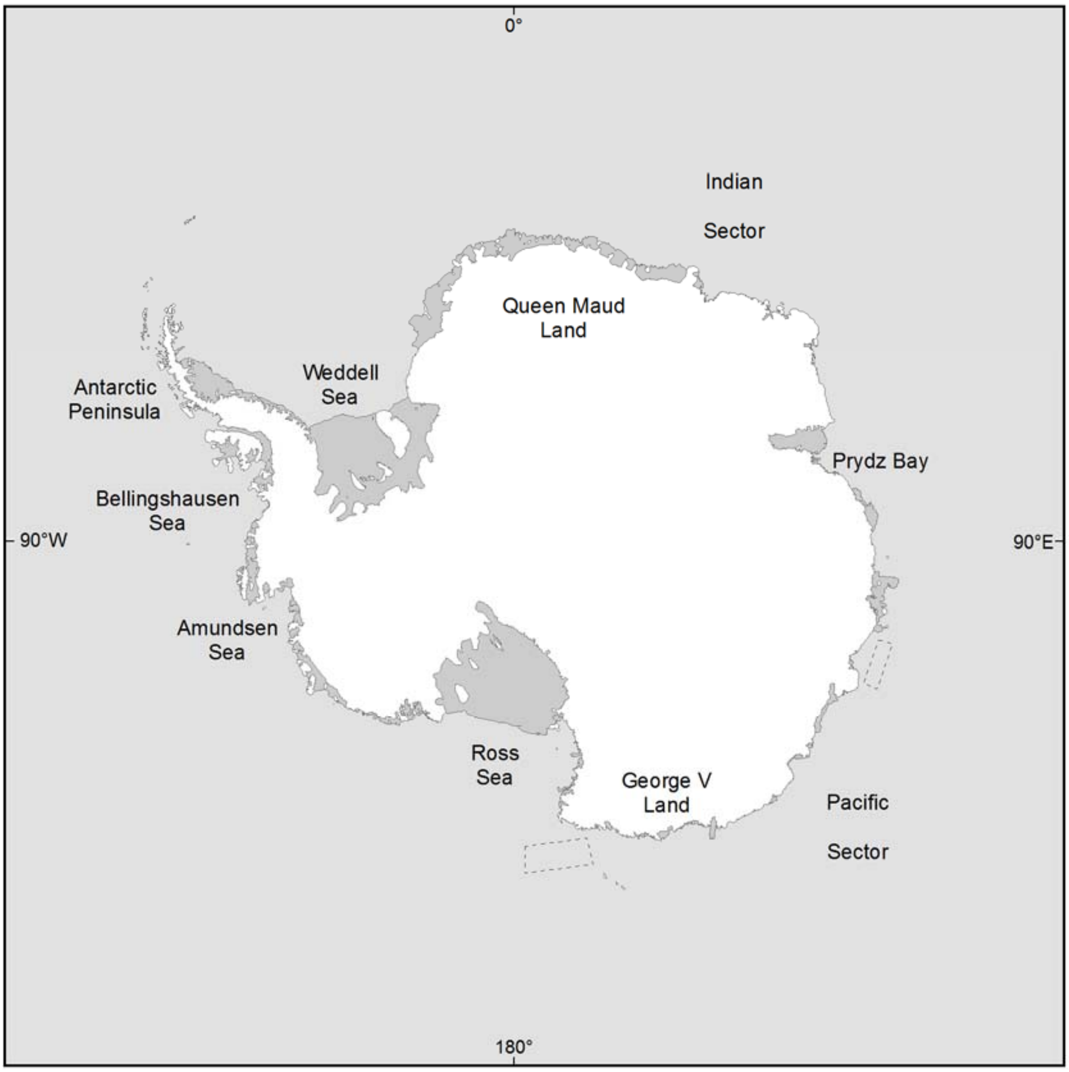

Figure 1: Areas surveyed by Eklund and Atwood (1962). Some of the place names in the text are shown.

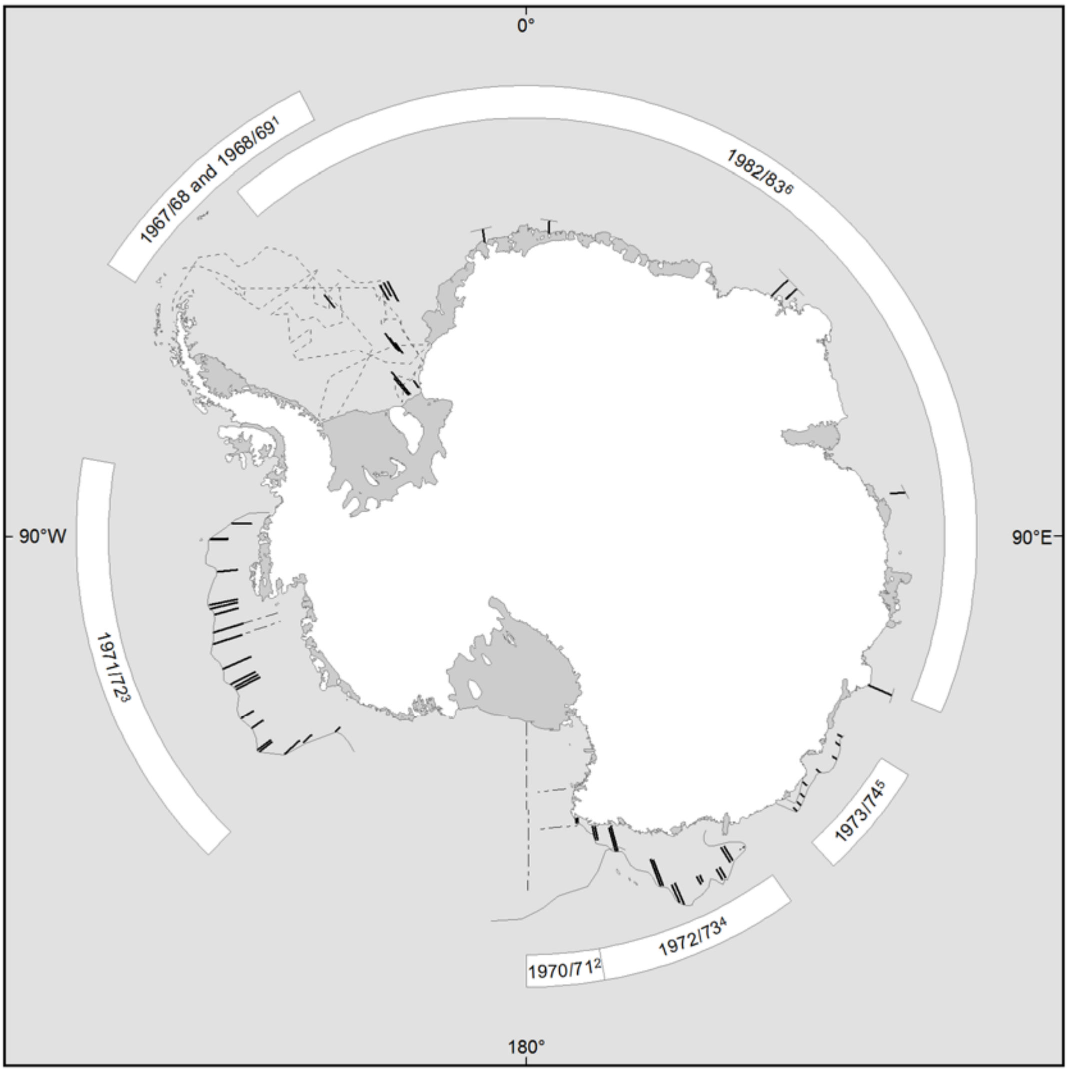

Figure 2: Transect locations (ship sighting transects: dash lines; aerial photographic transects: dash-dot lines; aerial sighting transects: bold lines) in relation to the ice edge at the time of surveys (not shown for Weddell Sea, light line elsewhere) for 'Erickson' surveys from 1967/68 to 1982/83. [1] Erickson et al. (1969), Siniff et al. (1970); [2] Gilbert and Erickson (1977); [3] Erickson et al. (1972), Gilbert and Erickson (1977); [4] Erickson et al. (1973), Gilbert and Erickson (1977); [5] Erickson et al. (1974); [6] Erickson et al. (1983).

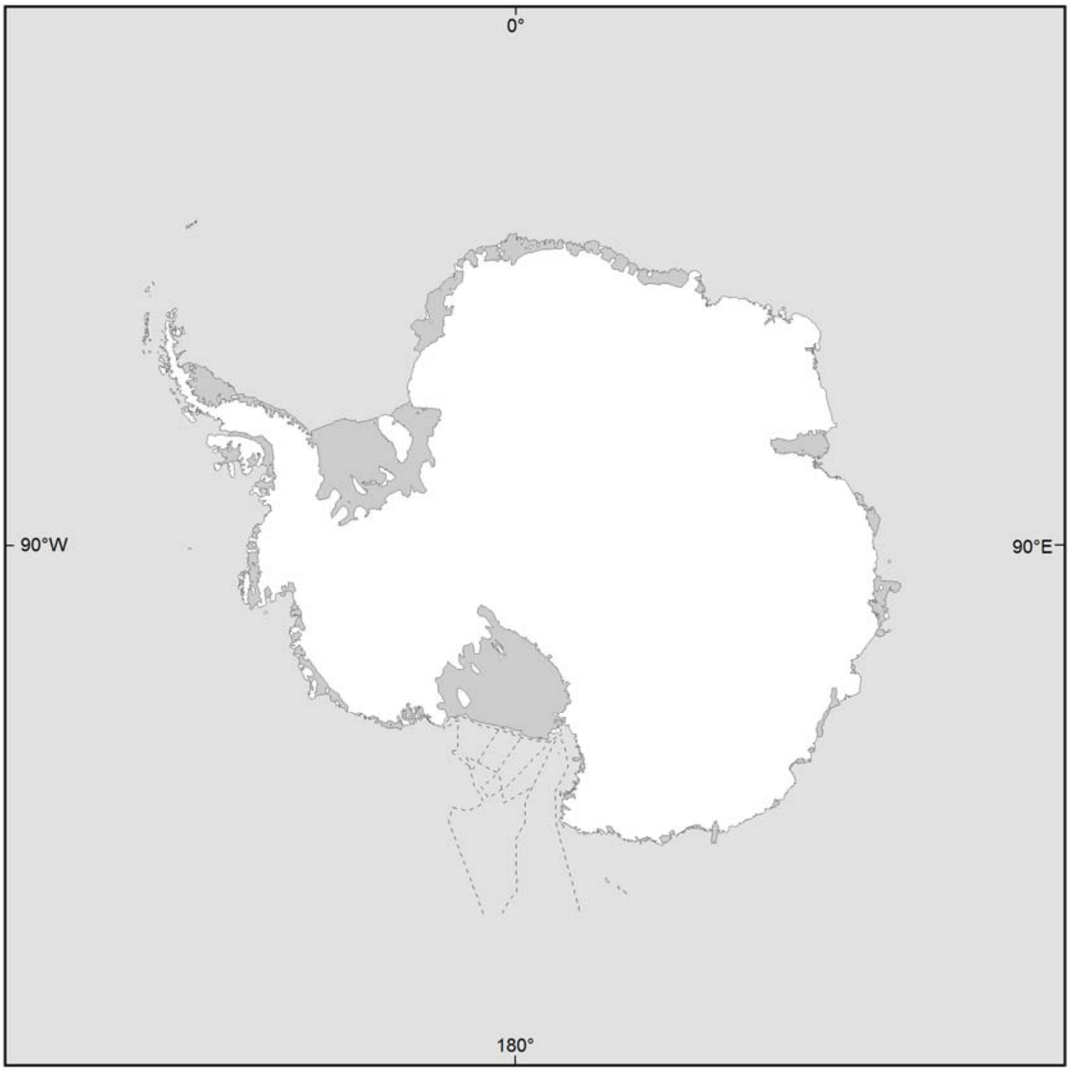

Figure 3: Transect locations in the Ross Sea for surveys by Ainley (1985).

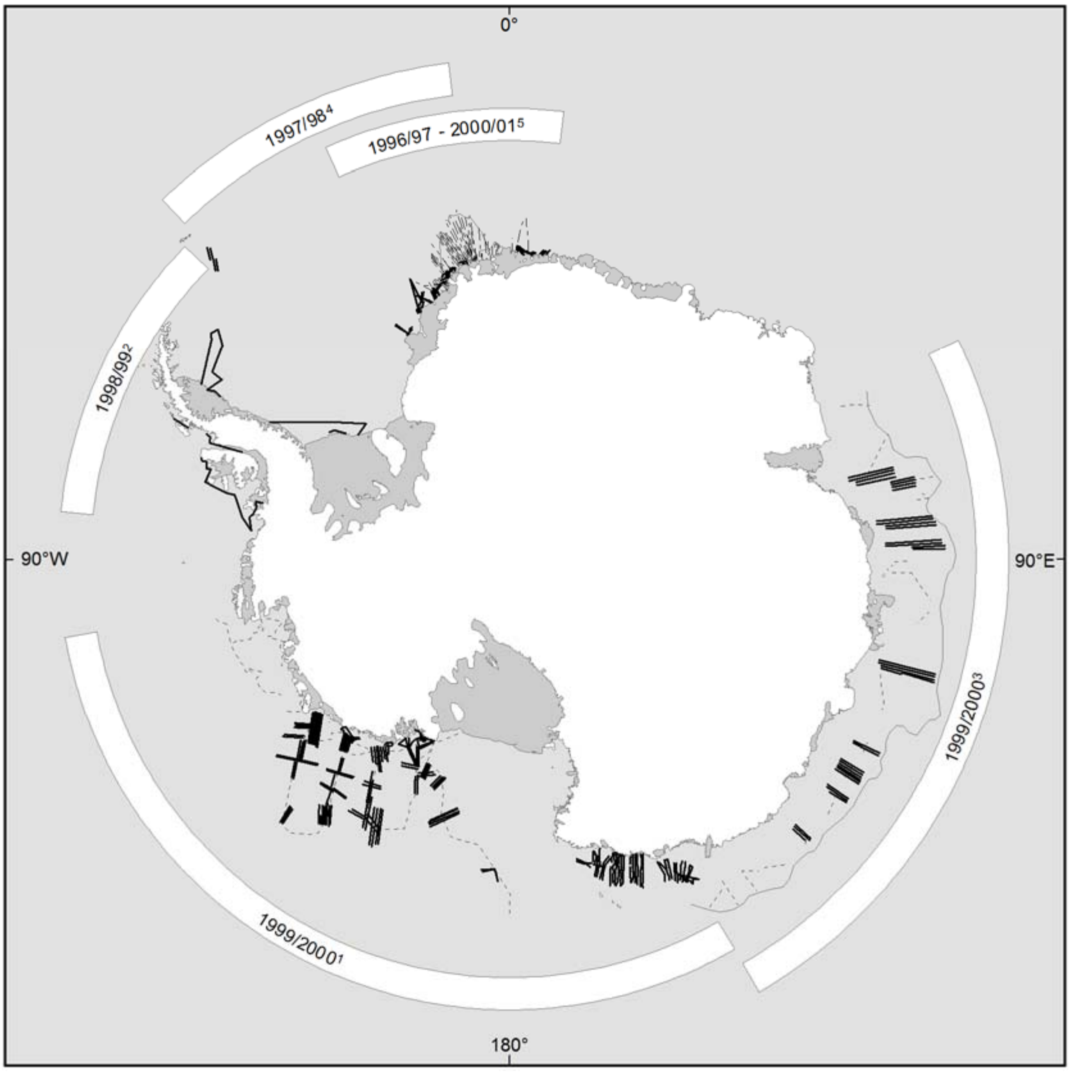

Figure 4: Transect locations (ship sighting transects: dash lines; aerial photographic transects: dash-dot lines; aerial sighting transects: bold lines) for APIS surveys from 1996/97 to 2000/01. Ice edge at the time of survey from 60°E–150°E shown as a light line. [1] Bengtson et al. (2011); [2] Forcada and Trathan (2008); [3] Southwell et al. (2008a, 2008b, 2008c); [4] Bester and Odendaal (2000); [5] Blix (pers. comm.); Plötz (pers. comm.).