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ORIGINAL PAPER

Movements and dive behaviour of two leopard seals (*Hydrurga leptonyx*) off Queen Maud Land, Antarctica

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Abstract Two adult female leopard seals (*Hydrurga leptonyx*) were tagged with satellite-linked dive recorders off Queen Maud Land, Antarctica, just after moulting in mid-February. The transmitters transmitted for 80 and 220 days, respectively. Both seals remained within the pack ice relatively close to the Antarctic Continent until early May, when contact was lost with one seal. The one remaining seal then migrated north, to the east side of the South Sandwich Islands in 3 weeks, whereafter it headed east, until contact was lost at 55°S in early September. From mid-May to late September this animal always stayed close to the edge of the pack ice. Both seals made mostly short (<5 min) dives to depths of 10–50 m and only occasionally dove deeper than 200 m, the deepest dive recorded being 304 m. A nocturnal diving pattern was evident in autumn and early winter, while day-time diving prevailed in mid-winter. Haul out probability was highest at mid-day (about 40% in late February and more than 80% in March and April). From May till September the remaining animal mainly stayed at sea, in the vicinity of the pack ice, with only occasional haul outs. These data suggest that a portion of the adult leopard seals may spend the winter mainly in open water, off the edge of the pack ice, where they primarily hunt near the surface. In that case, it is likely that krill (*Euphausia superba*), as well as penguins, young crabeater seals (*Lobodon carcinophaga*) and a variety of fish are important prey items.

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Introduction

The leopard seal (*Hydrurga leptonyx*) is a solitary animal that is frequently seen all around the Antarctic Continent, but it is nowhere common. The animal is mostly found within 300 m of the edge of the pack ice, or near leads and polynias close to the Antarctic Continent, during austral summer (Condy 1977; Bester et al. 2002), when most observations of this elusive animal have been made. Rogers et al. (2005) studied for the first time the spatial distribution of 11 adult leopard seals in the Prydz Bay area by use of satellite tags and found that they stayed within 320 km of the tagging site. It is well known, however, that the sub-Antarctic islands, like South Georgia, Kerguelen, Heard and Macquarie, are frequently visited by leopard seals during austral winter, and, in spite of the fact that only four of their animals transmitted for more than 2 months, Rogers et al. (2005) argued that those that migrate north are primarily juvenile animals (Walker et al. 1998; Forcada and Robinson 2006), while their own animals showed behaviour more typical of adults.

Kuhn et al. (2006) have provided the one and only study of leopard seal diving behaviour in one juvenile off the coast of the Antarctic Peninsula in August and found that it stayed in the same area for 3 weeks, while performing short (<2 min) and shallow (<40 m) dives. Based on this information they argued against the commonly held belief that krill (*Euphausia superba*) is the primary prey of leopard seals during winter (e.g., Øritsland 1977; Hofman et al. 1977; Lowry et al. 1988), since the krill were found at deeper depths at that time (Ashjian et al. 2004; Lawson et al. 2004). Moreover, Walker et al. (1998) have reported that Antarctic fur seals (*Arctocephalus gazella*) and penguins are important prey for leopard seals that haul out along the beaches of the sub-Antarctic islands during winter, but that does, of course, not imply that penguins and fur seals are important for those that do not.

The above clearly demonstrates that information on leopard seal annual distribution, diving behaviour and diet is scarce, while the art of speculation has been prominent. In the present study, we obtained data that shed new light on winter location, diving behaviour, haul out of leopard seals from two adult animals that were tagged with satellite-linked dive recorders (SDRs) in mid-February off the coast of Queen Maud Land.

Materials and methods

Capture and tagging

In the period between 6 and 17 February 2001, 19 leopard seals (*H. leptonyx*) were located by helicopter in the pack ice off Queen Maud Land, Antarctica (69°S, 1–2°W), during the Norwegian Antarctic Research Expedition (NARE 2000/01). Sixteen of these were observed and inspected at close range in the period between 14 and 16 February. Of these, four had not finished moulting, nine took to the water and escaped before they could be immobilized, and one was found unsuitable for tagging for other reasons. The two remaining adult leopard (♀) seals were immobilized by use of an intra muscular injection of tiletamine-zolazepam ($\sim$1.0 mg·kg $^{-1}_{\text{bodymass}}$) Zoletile100, Reading, L'Hay-Les-Roses, France, delivered by use of a dart gun, measured (standard body length), (Table 1) and equipped with SDRs, on their heads according to the general procedures described by Blix and Nordøy (2007).

Satellite-linked dive recorders

The tags were 9 cm × 7.5 cm × 3.5 cm, 335 g, epoxy-casted 0.4 W SDR-T16 (Wildlife Computers, Redmond, WA, USA), powered with 2 C-cells, giving an expected transmission capacity of 60,000 transmissions, and had a 0–1,000 m range pressure transducer with a depth resolution of ± 4 m. Saltwater switches ensured that transmission only occurred while the seals were at the surface. The SDRs transmitted with an approximate repetition rate of one transmission every 50 s when wet and one every 90 s when dry. The SDRs operated on a daily basis with a daily allowance of 200 transmissions.

Data collection

The SDR units sampled time and pressure (depth) every 10 s and stored derived values of dive depth (DEPTH; maximum depth of a dive) and dive duration (DURATION) into bins with ranges that were user-defined before SDR deployment. Programmed bin ranges for dive DEPTH were: 12–52 m (1), 52–100 m (2), 100–200 m (3), 200–300 m (4), 300–500 m (5), >500 m (6) and for DURATION 0–5 min (1), 5–10 min (2), 10–15 min (3), 15–20 min (4) 20–30 min (5), >30 min (6). Binned data were collected into 6-h DEPTH and DURATION histograms. Histograms were generated for the periods 21.00–03.00 (night), 03.00–09.00 (morning), 09.00–15.00 (day), 15.00–21.00 (evening), (GMT + 1 h, local time). The transmitters also collected information on daily haul out pattern by TIMELINE messages, where each timeline message covers a 24-h period (midnight–midnight). The 24 h are divided into 20-min increments, and the SDR assesses the conductivity readings for each 20-min period and reports whether the majority of the readings during that 20-min period were "wet" or "dry". The collected data were stored until transmitted and relayed via polar-orbiting National Oceanic and Atmospheric Administration satellites, using the CLS Argos system.

Location data analyses

CLS Argos assigns a location class (LC = 3, 2, 1, 0, A or B) to the calculated locations which indicates the accuracy of the location, LC 3 being the most accurate with 68% of the calculated latitudes and longitudes guaranteed to be within 150 m of true location. CLS Argos does not give guarantees with regard to the accuracy of locations of LC = 0, A or B, which tend to predominate in marine

Table 1 Details on seal number, sex and size (standard body length) as well as position and date of tagging, date of last location/uplink and calculated longevity for two adult leopard seals tagged off Queen Maud Land, Antarctica, in February 2001

Seal #	Sex	Standard body length (cm)	Tagging position	Tagged (dd-mo-yy)	Last location (dd-mo-yy)	SDR longevity (days)
1	F	311	69°28′S 01°46′W	14-02-01	04-05-01	80
2	F	280	69°29′S 01°28′W	16-02-01	23-09-01	220

mammal studies (e.g., Nordøy et al. 1995; Folkow et al. 1996). However, a study on grey seals (Vincent et al. 2002) suggests that the quality of LC = A may be quite acceptable, and even the quite poor accuracy of LC = B may be of interest in dealing with the distribution of seals that make large-scale movements within relatively short periods of time.

Ice charts

Information on pack ice coverage and distribution was obtained from the U.S. Navy/NOAA joint Ice Center (Naval Polar Oceanography Center), Washington, DC.

Results

Animals and tag performance

Based on data for the relationship between standard length and body mass from various sources (Hofman et al. 1977; Nordøy and Blix unpublished; Kuhn et al. 2006), the body mass of the two leopard seals that were tagged, were estimated to 320 and 400 kg, respectively, and judged to be adults. The two tags lasted 80 (seal #1) and 220 (seal #2) days, respectively (Table 1).

Diving duration and dive depth data for a total of 26,622 and 23,951 dives, respectively, were collected into 917 and 845 DURATION and DEPTH histograms. Based on these histograms, data on diving behaviour was obtained for about 73% of the tracking period. A total of 811 (seal #1) and 1,021 (seal #2) locations were obtained. Overall, 28.2% of the locations were of LC > 0, 21.9% of LC = 0, 21.4% of LC = A, and 28.4% were of LC = B. Tracks of individual seals were constructed based on LC = A, or better. On average, the two seals were located on 88% of the days that the transmitters were active.

Seal movements

Figure 1 shows an overview of the movements of the leopard seals between 14 February and 23 September 2001. Both seals remained in the pack ice the first few days after tagging, but left the ice edge on 20–22 February for a period of 10 and 14 days, respectively, reaching 67° 40′S in open water (Fig. 2). During the first week of March they both returned to the pack ice and hauled out regularly. In late March both seals moved SW into the Weddell Sea, whereafter they began to move north with the expansion of the pack ice while hauling out at mid-day in early April (Figs. 2, 3). In May and June the one remaining seal continued to move north, passing the eastern side of the South

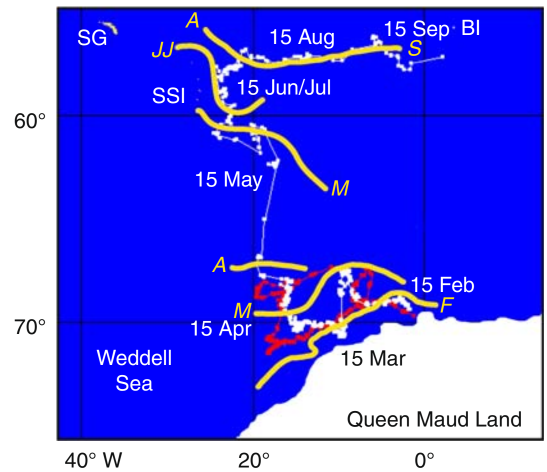

Fig. 1 Movements of two female leopard seals tagged with satellite-linked dive recorders in the pack ice off Queen Maud Land. The two tracks show the movements between 14 February and 23 September. The tag of leopard seal #1 (*red track*) stopped transmitting on 5 May, while the tag of seal #2 (*white track*) stopped transmitting on 23 September. Monthly average pack ice distribution (ice class 4 or higher) is shown by *yellow lines* and months are indicated by *capital letters*. *SG* South Georgia, *SSI* South Sandwich Islands

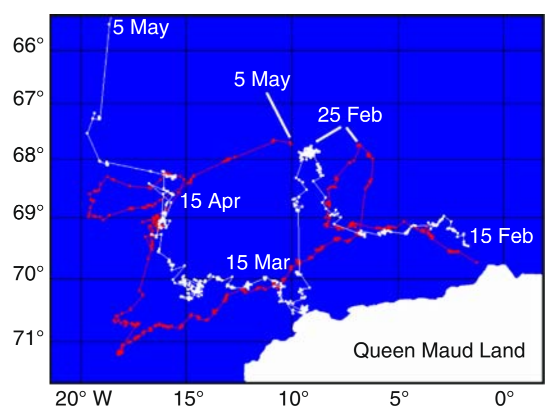

Fig. 2 Details of the movements of the two adult female leopard seals shown in Fig. 1. The two tracks (in *red* and *white*) show the period between 14 February and 5 May, when contact was lost with one of the transmitters (*red track*). The tracks are based on all daily average locations of class (*LC*) A and better

Sandwich Islands (Fig. 1) in June, to reach 57°S by the end of the month. In July, it remained fairly stationary at this latitude between 20 and 25°W before it ventured due east in August and September along the edge of the pack ice until contact was lost, south of Bouvet Island on September 23 at 2°E, having reached its farthest north at 55°S on 9 September (Fig. 1).

Seal #1 travelled a distance of 3,300 km (#2 had travelled 3,900 km at the same time) in the 80 days it was tracked, giving an average travel speed of 1.7 km h^{-1},

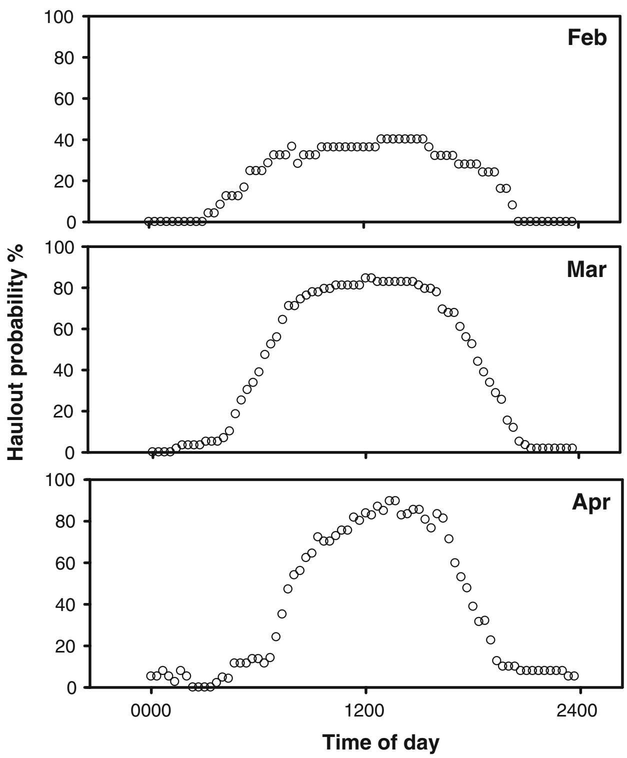

Fig. 3 The monthly (February, March and April) average diurnal haul out probability of two female adult leopard seals. The data are based on the timeline haul out messages obtained from the SLDR's

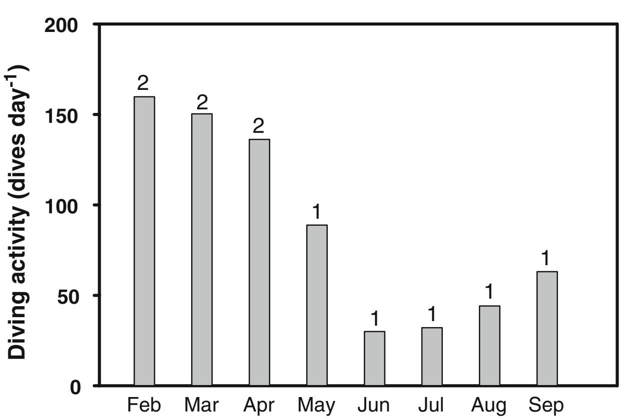

Fig. 4 Monthly average diving activity (dives day^{-1}). The bars represent an average of the two seals in the period February–May. Only dives deeper than 12 m are included

while seal #2 travelled a total of 9,500 km in 220 days, giving an average travel speed of 1.8 km h^{-1}.

Diving behaviour

Diving activity

The leopard seals were diving (deeper than 12 m) at a high rate of 160 dives day^{-1} after tagging in February and

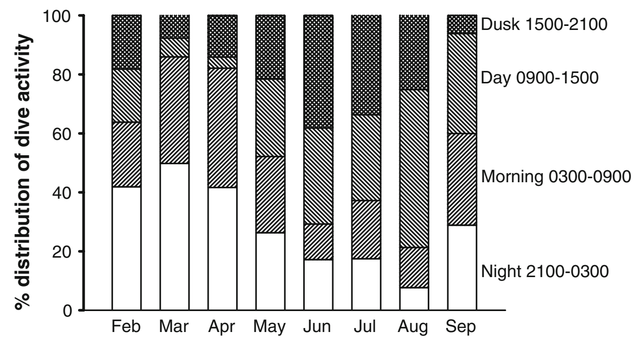

Fig. 5 The monthly average per cent distribution of diving activity between four time periods of the day: morning (03.00–09.00); day (09.00–15.00); dusk (15.00–21.00) and night (21.00–03.00). *Bars* show the average of two seals for the period February–May

maintained a high rate of diving activity in March and April, dropping off in May, to reach the low level of 30–40 dives day^{-1} in mid-winter (June–August) (Fig. 4).

Diel diving activity

During the very active period of diving in February–April, 40–50% of the dives were done in the 6-h night-time period (21.00–03.00), while only 5–15% were done at day-time (09.00–15.00) (Fig. 5). In mid-winter, however, the remaining seal instead became more active at day-time with as much as 50% of its dives during day-time and only 5–10% during night-time in August.

Haul out

During February–April both seals had maximum haul out probability at mid-day. Thus, in February, the mid-day haul out probability was about 40%, increasing to 80–90% in March and April (Fig. 3). The haul out probability continued to be at a maximum in midday until contact was lost in September in the one remaining animal. During this period, however, the mid-day haul out probability was only around 50%, and while the animals hauled out almost every day in February–April, the remaining animal often were at sea for several days at a time, and haul out only occurred in 30–50% of the days, in May–September. From the timeline haul out data it can, moreover, be estimated that the two leopard seals hauled out in pack ice for an average of 5 h per day in February, increasing to 11 and 8 h per day in March and April, respectively.

Diving duration and depth

The monthly overall relative distribution of diving durations and diving depths is shown in Fig. 6a, b. During the

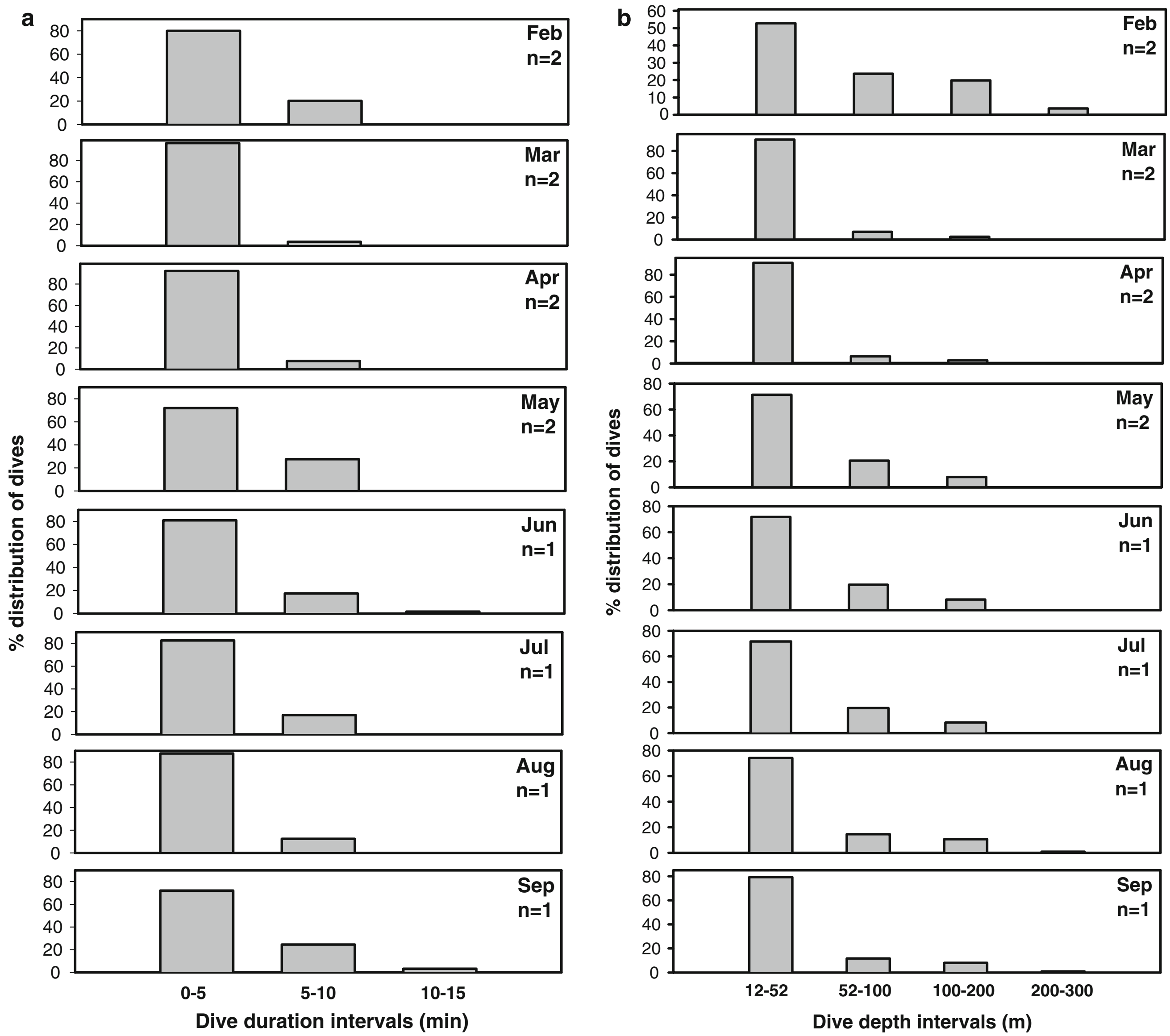

Fig. 6 Overall frequency (% distribution) of dive duration (**a**) and dive depth (**b**) of two female leopard seals. Diagrams for the period February–May are averages for the two seals

entire period from February to September short duration dives of less than 5 min dominated and contributed 70–90% of all dives. A significant proportion of dives (5–25% on a monthly basis) were of 5–10 min duration, but only one dive was longer than 15 min (Fig. 6a).

The monthly overall relative distribution of dive depths (Fig. 6b), clearly indicates that the leopard seal is a shallow diver with as much as 50–90% of the dives shallower than 52 m for the entire period between February and September. In February, there was a tendency towards deeper diving, compared to the other months, with some 25% of dives in the 100–300 m depth interval, but in March and April the seals were diving shallower and less than 10% of all dives were deeper than 52 m. In the period May-September, the fraction of deeper dives again increased, but still less than 25% of dives were deeper than 52 m, and less than 1% were in the 200–300 m depth interval.

Maximum daily dive depth

Individual maximum daily dive depth varied considerably, from only 8 to 304 m, the latter being the deepest dive recorded in this study (Fig. 7). Average maximum daily dive depth was 140 ± 8 m (SEM, $n = 68$) and 108 ± 7 m (SEM, $n = 93$) for the two seals, respectively.

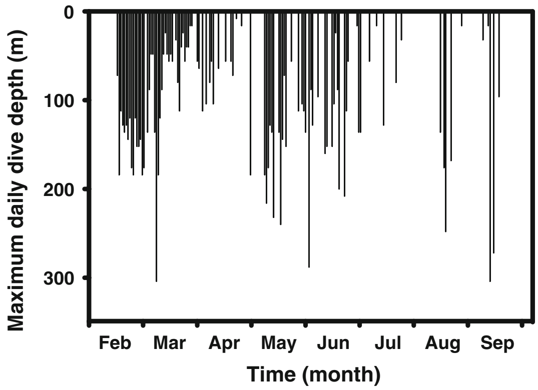

Fig. 7 Maximum daily dive depths (m) for a female leopard seal (#2/01) for the period 16 February–23 September, the deepest dive on record being 304 m

Discussion

Capture and tagging method

Of the 16 "adult-sized" leopard seals that were approached at close range in mid-February, at least, 4 were still in a very early stage of moulting. It is worth noticing that in the study by Rogers et al. (2005) the tags that were deployed in November and December stopped transmitting in January, and the two tags that lasted much longer than the others were deployed on 3 and 14 February, respectively, which is about the same time we deployed our tags. This suggests that moulting takes place in the latter part of February in the Queen Maud Land sector, a notion which is further supported by the fact that, in ship surveys undertaken from 23 January–30 January and aerial surveys undertaken from 31 January–17 February no leopard seals were observed until 6 February, while Ross seals (*Ommatophoca rossii*) were observed repeatedly throughout the entire period (Nordøy and Blix unpublished).

The two tags that were deployed stopped transmitting after 80 and 220 days, respectively. At that time plenty of battery power remained and only 75% of the programmed number of bytes had been spent even at day 220. These durations are considerably shorter than what we achieved with most of our Ross seals, that were tagged in the same place and season (Blix and Nordøy 2007). Rogers et al. (2005), however, obtained longevities of a similar distribution as in the present study. Given our long experience in using satellite tags, and our exceptional success of their deployment on Ross seals in the same season, we can only assume that some sort of mechanical failure, or the demise of the animal, was the reason for the relatively short longevity of the tags.

Movement patterns

After tagging in mid-February our animals moved west (Fig. 1), probably due to the westward movement of the ice, caused by prevailing westerly winds and currents in this area, that may reach a speed of 10 km day^{-1} (Fahrbach et al. 1992; Harms et al. 2001). In late February both seals left the ice for the open ocean for a 2-week period, before they returned to the pack ice in early March, whereafter they moved further west into the Weddell Sea, all the time in contact with the pack ice. This initial movement pattern is reminiscent of that of the crabeater seal in the same area in 1993 (Nordøy et al. 1995) and in 1997 (Nordøy and Blix unpublished), but differs remarkably from that of the Ross seal (Blix and Nordøy 2007). Thus, so far, the movements of our leopard seals did not differ all that much from those of the animals studied by Rogers et al. (2005). But, contrary to their findings, our two seals started to move north with the expansion of the pack ice in April, and the remaining seal reached the area east of the South Sandwich Islands in late June (Fig. 1), which is consistent with numerous observations over the last century of leopard seals at the sub-Antarctic islands in winter (Rogers et al. 2005, for several references). It is further important that this exodus to lower latitudes was not a "hit and run" operation on account of our animal, that continued to operate mostly in open water north of the pack ice for several months in mid-winter. The lack of such behaviour in the two animals studied by Rogers et al. (2005), that transmitted long enough to be relevant in this context, can therefore hardly be explained as a phenomenon typical of adult animals. So, obviously, much more is to be learnt about the winter distribution of the leopard seals.

Diving behaviour

This study has shown a striking reduction of the diving activity of the leopard seal down to only 20% of the summer values in mid-winter (Fig. 4). There is no other direct information in the literature about seasonal diving activity of leopard seals, but both Ross seals (Blix and Nordøy 2007) and crabeater seals (Nordøy et al. 1995) show a similar, but less pronounced, tendency towards reduced diving activity in mid-winter, being 53 and 60% of the summer value, respectively.

Diving duration and depth

The dive durations of our leopard seals were consistently short, 80–90% lasting less than 5 min (Fig. 6a), with only one dive recorded in the 15–20 min bin throughout the study period. This is similar to the 2 min average, and 9.35 min maximum, dive duration of the juvenile studied by Kuhn et al. (2006) in August, and seems to establish the leopard seal as the most short-time diving phocid seal in Antarctica.

The dive depths of our leopard seals were also consistently shallow, with more than 70% of all dives shallower than 52 m (Fig. 6b) in the entire period between March and September. This is again consistent with the data from the juvenile studied by Kuhn et al. (2006) for which 63% of all dives in August were less than 50 m. However, both our adult seals and the juvenile of Kuhn et al. (2006) occasionally did dive to depths between 300 and 400 m (Fig. 7).

Winter diet speculations

Based on the telemetry studies of Rogers et al. (2005), Kuhn et al. (2006) and the present, it is, of course, anybody's guess what the leopard seals eat at sea during winter. However, the winter location and diving behaviour of our animal, which was quite reminiscent of the winter location and diving behaviour of the crabeater seal, seems to indicate that krill might, indeed, be an important prey item during winter, as originally suggested by Øritsland (1977) based on analysis of stomach contents. It follows, that the suggestion of Kuhn et al. (2006), that krill is not important during winter, should, for the time being, only be applied to juveniles in near coastal waters. Even if, at the end of the day, it should turn out that krill, surprisingly, really is the winter diet of leopard seals, it is well documented that some of these animals supplement their diet at times with fur seal and crabeater seal pups, as well as with a variety of penguins (see: e.g., Walker et al. 1998; Hiruki et al. 1999, for numerous references). In this context, it is tempting to suggest that the reason for the few and seemingly senseless deep dives of the leopard seal might be caused by an occasional "hot pursuit" of such animals, or, alternatively escape from predators, such as killer whales (*Orcinus orca*).

Haul out behaviour

In late February the mid-day haul out probability of our two animals was only about 40%, but increased to about 80% in March and April, with a haul out probability of close to zero during mid-night for the whole period (Fig. 3). This mid-day haul out during summer is consistent with our observations of a low diving activity during the day (Fig. 5) and with the observations of Gilbert and Erickson (1977), Rogers and Bryden (1997) and Hiruki et al. (1999). But, the low haul out probability in February, possibly also in mid-summer, when population censuses are often carried out, has not been known, and may imply that existing population estimates for this species are considerably undervalued.

Leopard seal abundance

In a recent paper Southwell et al. (2008) raise the question of whether the leopard seals are uncommon or cryptic based on the finding of only 12 sightings in 5,978 km of aerial surveys in east Antarctica, from 4 December to 10 January, which is supposed to overlap with the breeding season of the species. In the present study we made 16 definite sightings in 3 days of modest aerial survey effort from 14 to 16 February, which is supposed to overlap with the moulting season of the species. Southwell et al. (2008) expressed concern that not all animals were available for survey at the time of their effort, and the present study may indicate that a significant proportion of the population could have been at sea at the time, and that the best time for surveys of leopard seals is February–March rather than December–January.

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