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Diving physiology and winter foraging behavior of a juvenile leopard seal (*Hydrurga leptonyx*)

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Abstract Diving physiology and at-sea behavior of a juvenile leopard seal (*Hydrurga leptonyx*) were opportunistically measured in the Antarctic Peninsula during winter 2002. Total body oxygen stores were estimated from measures of hematocrit, hemoglobin, myoglobin, and total blood volume and were used to calculate an aerobic dive limit (ADL). Movement patterns and diving behavior were measured by equipping the seal with a Satellite Relay Data Logger that transmitted data from 8–31 August 2002. The seal remained in a focal area, in contrast to crabeater seals tracked simultaneously. The seal displayed short, shallow dives (mean 2.0 ± 1.4 min, 44 ± 48 m) and spent 99.9% of its time within the estimated ADL of 7.4 min. The shallow diving behavior contradicts previous diet research suggesting Antarctic krill (*Euphausia superba*) is the primary prey of leopard seals during the winter months as krill were found at deeper depths during this period. These measurements of diving and movement of a leopard seal provide valuable preliminary data necessary to develop future research on the at-sea behavior of an apex predator in the Antarctic ecosystem.

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Introduction

Pack ice seals of the Antarctic (crabeater [*Lobodon carcinophaga*], Ross [*Ommatophoca rossii*], and leopard seals [*Hydrurga leptonyx*]) comprise over 50% of the world's pinniped population (Laws 1984). Yet because of their distribution in the heavy pack ice and the harsh environment of the Antarctic, access to these animals can be limited and research at times can be impossible. Winter access to this region is even more problematic and consequently little is known about the wintertime movement and behavior of many Antarctic species.

The ecology of leopard seals is of significant importance to our understanding of the Antarctic ecosystem because they are apex predators that regularly feed on organisms from multiple trophic levels including krill, fish, penguins, and other seals (Hofmann et al. 1977; Lowry et al. 1988). During winter months, adult leopard seals are thought to prey primarily on Antarctic krill (*Euphausia superba*), an abundant resource also consumed by crabeater seals and Adèlie penguins (*Pygoscelis adeliae*) (Green and Williams 1986; Lowry et al. 1988; Walker et al. 1998). Other than diet analysis and restricted observational studies (Hofmann et al. 1977; Green and Williams 1986; Lowry et al. 1988; Walker et al. 1998) almost nothing has been published about the physiology and/or diving behavior of free-ranging leopard seals. This study examined the physiology, diving behavior, and movement pattern of a leopard seal during the austral winter of 2002, off the Antarctic Peninsula.

Materials and methods

As part of a research program (Southern Ocean GLOBEC) to study the foraging ecology of crabeater seals, we opportunistically studied the behavior and physiology of one juvenile male leopard seal in August 2002. The seal was captured on the pack ice north of Adelaide Island ($66^{\circ} 51.6^{\circ}\text{S}$, $66^{\circ} 24.3^{\circ}\text{W}$), along the Western Ant-

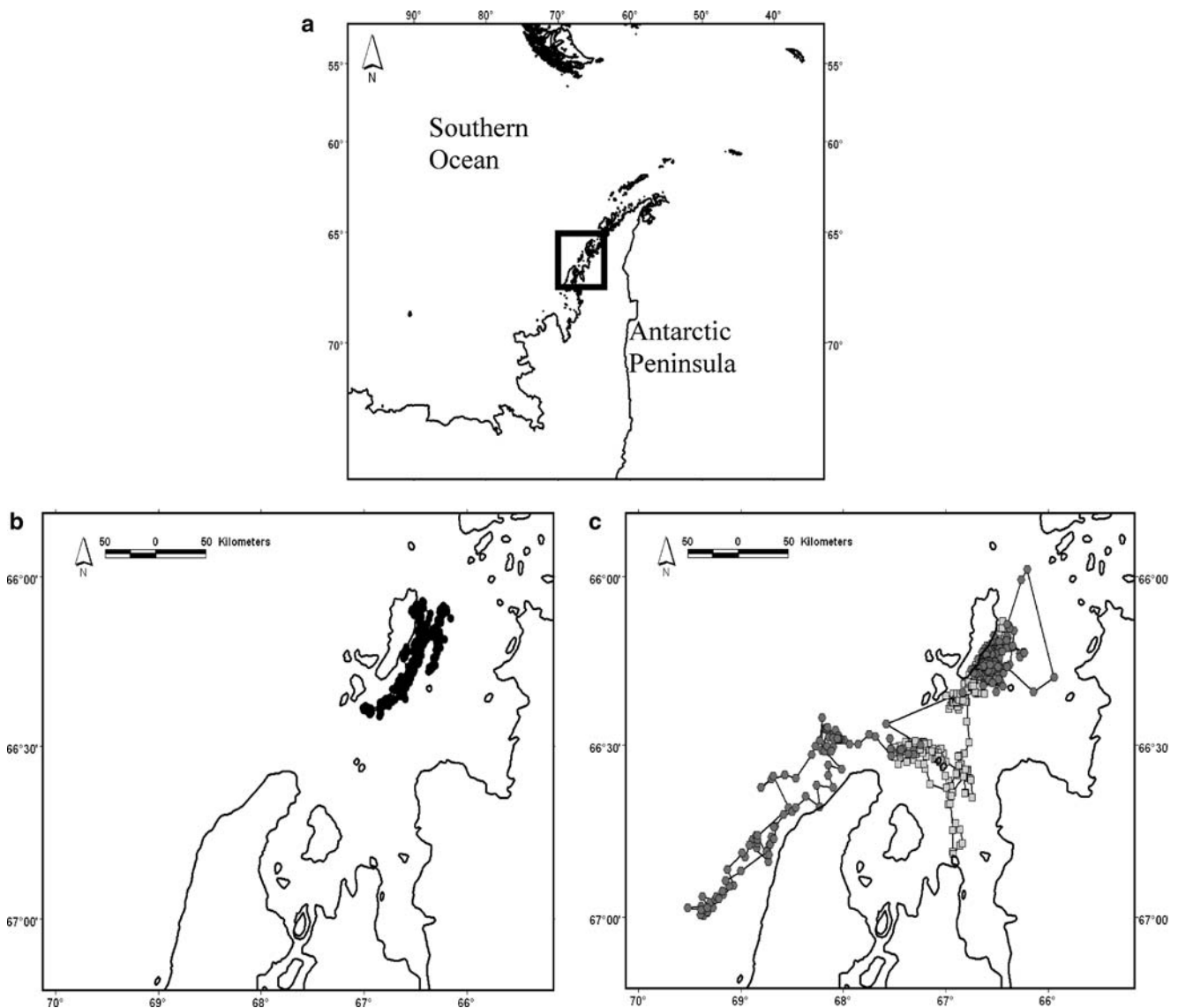
arctic Peninsula (Fig. 1a). The seal was initially sedated with 200 mg Telazol (Fort Dodge, USA) injected intramuscularly using a pole syringe. The seal was then physically restrained with a net for anesthetic induction with isoflurane via a mask using a field portable gas anesthesia machine.

The seal was weighed in a sling, using a hand winch and scale (Ohaus I-20W, capacity $1,100 \pm 0.5$ kg). Body composition was determined using the truncated cones method by measuring blubber depth with a portable ultrasound scanner (Scanoprobe II, USA) and taking length and girth measurements following methods

described elsewhere (Gales and Burton 1987; Worthy et al. 1992).

Total blood volume was calculated from measures of hematocrit (Hct) and plasma volume (Pv, ml). Plasma volume was determined using Evan's blue dye injected intravenously following standard methods (El-Sayed et al. 1995; Costa et al. 1998). Total blood volume (Bv, ml) was then calculated as: $Bv = Pv / [100 \times (1 - Hct)]$. Hemoglobin concentration was measured colorimetrically at 540 nm using a spectrophotometer after adding 10 μ l of whole blood to 2.5 ml of Drabkin's reagent (Sigma Chemicals kit 625A). To determine muscle oxygen stores, a sample of tissue was obtained from the latissimus dorsi muscle by making a 1 cm incision, then using a biopsy needle. Muscle myoglobin concentrations were measured according to methods described by Reynafarje (1963). Finally, results from the above assays were used to calculate total body oxygen stores to predict the aerobic capacity of the seal while diving (aerobic dive limit, ADL)

Fig. 1 **a** Region of the Antarctic Peninsula where research was conducted (denoted by *black square*). **b** Argos locations from the juvenile leopard seal from 8 August–31 August 2002. **c** Argos locations from two representative crabeater seals (*light gray squares and dark gray circles*). Note all four crabeater seals tracked traveled over a more extensive area despite similar tagging location and tracking duration (24 days)



following equations published in Kooyman and Sinnet (1982) and Ponganis et al. (1993).

Diving behavior and movement patterns were examined by equipping the seal with a Satellite Relay Data Logger (SRDL; Sea Mammal Research Unit, St. Andrews Scotland). The instrument was glued to the head with fast setting epoxy (Devcon 5 min.). The SRDL collected and summarized data on the animal's behavior and transmitted this information via the ARGOS satellite system (Fancy et al. 1988). The SRDL sampled depth, temperature, condition (wet/dry), and swim speed at 4 sec intervals and provided locations for all satellite uplinks. The SRDL summarized behavior into three mutually exclusive categories: diving, hauled out, or cruising. Diving was identified when the tag was at depths below 6 m for more than 8 s. Haul outs were classified as periods when the animal was out of the water for more than 10 min. Cruising was identified when the animal was in the water and no dives occurred. The transmitted data included summary information (time spent in each behavior during 4 h intervals) as well as detailed dive information for all dives (depth, duration, and an index of dive shape). Further details on tag programming and tag descriptions are available in Fedak et al. 2001, 2002 and Burns et al. 2004.

Dive data were filtered to remove erroneous readings using descent and ascent rates as described in Burns et al. 2004. Satellite locations were filtered using a maximum travel speed of greater than 4.0 m s^{-1} (McConnell et al. 1992), and location data were analyzed using ArcView GIS 3.2, Animal Movement Program 2.04 and Spatial Analyst 2.0. Minimum convex polygon (MCP) analysis was conducted using all remaining Argos locations to calculate the area used by the leopard seal. For comparison of movement patterns, MCP analysis was also performed on data from four crabeater seals previously summarized in Burns et al. 2004. The crabeater seals were tagged in the same location as the leopard seal (5–7 August 2002) and were tracked for the same number of days. This comparison provided the opportunity to evaluate the simultaneous movements of two species, thought to forage on the same prey resources. For the first time, we were able to obtain a glimpse of how these species may reduce interspecific competition.

Summary data for movement, diving, haul out, and cruising patterns are reported as mean \pm SD. To compare day and night dive depths, data were \log_{10} -transformed to normalize the data and ensure equal variances. A two-sample t-test was used to compare groups and data were considered significantly different at $P < 0.05$ (SYSTAT 10, SPSS Inc., USA).

Results and discussion

The mass of the seal was 197.5 kg, axillary girth 143 cm, and standard length 227 cm. Based on length, this individual was classified as a yearling (Hamilton 1939).

Body composition of the seal was 29.7% adipose tissue and 70.3% lean tissue. The plasma volume was 15.0 l, and total blood volume 25.9 l or 13.1% of the seal's mass. Hemoglobin, hematocrit, and myoglobin concentrations were $14.7 \text{ g } 100 \text{ ml}^{-1}$ blood, 42%, and $5.1 \text{ g } 100 \text{ g}^{-1}$ muscle, respectively. Total blood oxygen stores were $21.4 \text{ ml O}_2 \text{ kg}^{-1}$. Assuming a muscle mass of 35% (Ponganis et al. 1993), we estimated muscle oxygen stores to be $23.9 \text{ ml O}_2 \text{ kg}^{-1}$.

Lung oxygen stores were estimated from allometric equations of Gentry and Kooyman (1986), assuming a diving lung volume of 50% (Kooyman et al. 1971). Davis and Kanatous (1999) suggest for Weddell seals that spend much of their time below 50 m, lung oxygen stores are not available. However, based on the diving performance of this leopard seal, lung oxygen stores may be a valuable oxygen reserve during diving and were included in the calculations of total body oxygen stores. Therefore, using the sum of blood, muscle, and lung oxygen stores, we calculated mass specific total body oxygen to be $51.4 \text{ ml O}_2 \text{ kg}^{-1}$. Assuming a conservative metabolic rate of $1.19 \text{ l O}_2 \text{ min}^{-1}$ (two times Kleiber and Kooyman 1989) and using total available oxygen stores, the calculated ADL of the seal was 7.4 min (Ponganis et al. 1993; Davis and Kanatous 1999).

In comparison with other juvenile phocids, the leopard seal's mass specific blood oxygen stores were low, resulting in lower total body oxygen stores relative to body size. When comparing specifically blood oxygen stores, the leopard seal had half the oxygen storage capacity of 8 to 10 month northern elephant seals (*Mirounga angustirostris*, $42.8 \text{ ml O}_2 \text{ kg}^{-1}$, Thorson and LeBoeuf 1994) and yearling gray seals (*Halichoerus grypus*, $45.3 \text{ ml O}_2 \text{ kg}^{-1}$, Noren et al. 2005). However, when comparing mass specific body oxygen stores to other juvenile phocids, the differences are less dramatic. Yearling Weddell seals (*Leptonychotes weddellii*) have mass specific body oxygen stores of $55 \text{ ml O}_2 \text{ kg}^{-1}$, and 8-month old northern elephant seals have $68.8 \text{ ml O}_2 \text{ kg}^{-1}$ (Burns and Castellini 1996; Thorson and LeBoeuf 1994, respectively). This suggests that the physiological performance of diving leopard seals is inferior to other phocids. This was previously suggested based on hematocrit, hemoglobin, heart rate, and respiratory rate data collected on captive leopard seals (Williams and Bryden 1993).

The SRDL reported data for a total of 24 days (8–31 August 2002). During this period, 428 locations were acquired. Over 74% of the locations were associated with an estimated error of 1 km or less (Service Argos 1996). Mean ground speed for the leopard seal, calculated as the travel speed between two consecutive Argos locations while the animal was in water, was 0.82 m s^{-1} with 75% of travel speeds between 0 and 1.0 m s^{-1} .

The satellite track from the juvenile leopard seal showed the animal moved within a smaller focal area during the 24 days of tracking than did the four crabeater seals tagged at the same time. The seal traveled

a total distance of 458 km and remained within an area of 664 km² (Fig. 1b), whereas the crabeater seals tracked from the same location traveled more extensively with distances ranging from 788 to 971 km within total areas between 1,213 and 5,105 km² (Fig. 1c). The maximum distance traveled by the leopard seal from the tagging location was only 40.3 km which was within the range of the maximum distances traveled by adult leopard seals reported by Rogers et al. 2005 in Prydz Bay. Although adult leopard seals remained sedentary during winter months, they did use a larger area than this juvenile traveling on an average 137 km from tagging location (Rogers et al. 2005).

This seal was captured and tracked in the Crystal Sound region, an area of high abundance of zooplankton, penguins, and seals, all potential prey of the leopard seal (Lawson et al. 2004; Zhou and Dorland 2004). During the winter months this area is also known to be covered in dense pack ice (Perovich et al. 2004). Although we encountered extensive ice cover during the tagging period, we are confident the leopard seal was not constrained by the physical properties of the environment (ice cover) because the crabeater seals moved over a much wider area. The localized movements of this animal, similar to adults measured in Prydz Bay, potentially reflect directed foraging behavior in an area of abundant prey resources. We suggest this disparity in movement patterns between species indicate fundamental differences in how crabeater and leopard seals utilize the marine environment, and this difference warrants further investigation.

The leopard seal spent the majority of time hauled out (58.9% ± 44.2), followed by cruising (27.3% ± 30.6), and diving (13.7% ± 20.0). The majority of dives were shallow (63% less than 50 m) with only 13% exceeding

100 m, and 2% deeper than 150 m (maximum 424.5 m). Mean dive duration was also short (2.0 ± 1.4 min) yet the maximum dive duration was 9.35 min (Table 1). Based on the estimated ADL, the aerobic capabilities closely match the recorded diving behavior, as nearly all dives (99.9%) were shorter than the estimated ADL.

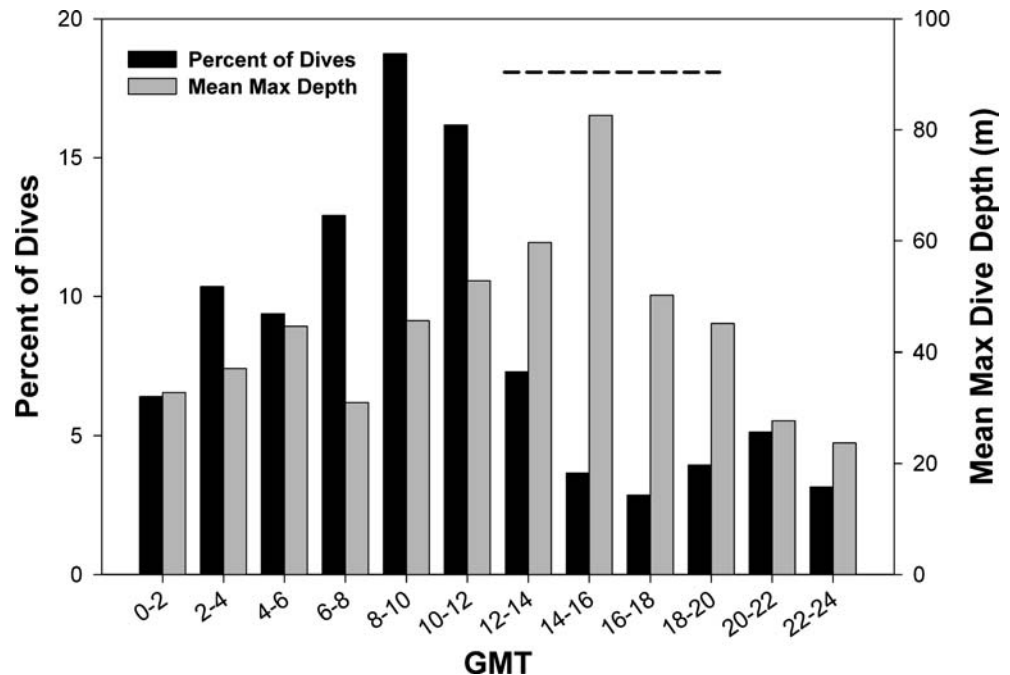
Both dive frequency and maximum dive depth for the leopard seal varied with the time of day (Fig. 2). The highest frequency of dives occurred during nighttime hours (as determined by local civil twilight) and peak activity occurred within the 4 h prior to sunrise (35% of dives between 0800 and 1200 GMT, Local time = GMT−3 h). In addition, mean dive depth was significantly deeper during daytime hours than during nighttime hours (day 59.6 ± 65.5 m, night 40.6 ± 42.7 m, P=0.003).

The measured diving behavior reflected a diel pattern, which is indicative of foraging on vertically migrating prey. Previous studies suggest that krill, a vertically migrating species, is an important component of leopard seal's diet during the winter months (Lowry et al. 1988). However, research conducted during the Southern

Table 1 Summary of diving and movement data recorded for 24 days in August 2002. Diving was identified when the animal was at depths below 6 m. Haul outs were classified as periods when the animal was out of the water for greater than 10 min. Cruising was identified when the animal was in the water, but no dives occurred

	N	Mean (SD)	Median	Range
Max dive depth (m)	1014	44 (48.0)	18	6–424.5
Dive duration (s)	1014	119 (82.6)	111	12–561
Surface travel (m/s)	160	0.82 (0.72)	0.59	0.01–3.44
Haul out periods (h)	14	13.7 (9.9)	13.2	0.3–28.6
Cruise time (min)	98	18.7 (18.1)	11	2–80

Fig. 2 Distribution of dive frequency and mean maximum dive depths during 2-h periods over the 24 day tracking period (Local time = GMT−3 h). The broken horizontal bar represents hours of local daylight. Note the largest number of dives occurred prior to sunrise and the deepest dives occurred during daylight hours



Ocean GLOBEC winter cruises in this area found large krill were absent from surface waters and were often associated with the bottom (Ashjian et al. 2004; Lawson et al. 2004). This suggests the leopard seal was not foraging primarily on krill because few dives were deeper than 100 m, in an area where bottom depths can exceed 400 m. Further research on the winter diet of leopard seals in the pack ice or juvenile seals may be able to resolve this inconsistency.

Although this research was based on a single juvenile individual, it sheds much needed light on the physiology, behavior, and movements of leopard seals. We believe these data can be useful to develop future avenues of research that investigate the behavior of leopard seals and are essential to understand the impact of this apex predator on the Antarctic environment.

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