ORIGINAL PAPER

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Movements and diving behavior of weaned Weddell seal (*Leptonychotes weddellii*) pups

Abstract Between 1993 and 1995, the diving behavior and movement patterns of 23 weaned Weddell seal pups (*Leptonychotes weddellii*) were tracked in the Ross Sea. Antarctica, using satellite-linked time-depth recorders. Regression analyses revealed that for seals of between 8 and 27 weeks old, age was poorly correlated with the dive depth, duration, or frequency. However, changes in dive parameters suggested that Weddell seal pups were attempting to maximize dive time, but the manner in which this was done depended on age and time of day. Movement patterns indicated that most Weddell seal pups left their natal area by the end of February, and traveled north along the Antarctic continent coastline. Several individuals returned to McMurdo Sound, but others were last located more than 400 km from McMurdo. Routes followed suggest that pups can use the pack ice habitat, but prefer to remain closer to the coastline than do adults.

Introduction

Most field-based studies of young marine mammals have concentrated on the lactation and/or the post-weaning period when most pups are relatively easy to find and observe (for review: Gentry and Kooyman 1986; Riedman 1990). Far fewer studies have focused on juvenile behavior after the animals have left the natal colonies (Lydersen and Hammill 1993; Thorson and Le Boeuf 1994; Burns and Castellini 1996; Le Boeuf et al. 1996;

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Burns and Testa 1997; Burns et al. Testa 1997; Horning and Trillmich 1997; Merrick and Loughlin 1997; Stewart 1997). In part, this has been due to the difficulties associated with finding, tracking, and monitoring animals that often remain at sea for long periods of time and travel over large areas. However, because juvenile survivorship in marine mammals is a critical factor in determining population size, studies of how behavior and physiology impact the survivorship of young of the year are vital (Eberhardt and Siniff 1977; Merrick et al. 1987; Hindell et al. 1991; Hastings 1996). Fortunately, recent advances in technology have reduced the size, weight, and cost of telemetry tags, while increasing their reliability and power output (Harris et al. 1990; Priede and French 1991; Costa 1993; Merrick et al. 1994, Service Argos 1996). This has made it possible to monitor remotely the behavior and movements of juvenile marine mammals as never before.

In McMurdo Sound, Antarctica, the diving behavior and population biology of Weddell seals (*Leptonychotes weddellii*) have been continuously studied for over 30 years (Smith 1965; Kooyman 1968; Stirling 1969; Kooyman et al. 1980; Thomas and DeMaster 1983; Testa 1987; Castellini et al. 1992; Testa 1994; Burns and Castellini 1996; Hastings 1996; Burns 1997). This research has revealed that juvenile diving behavior is affected by a combination of factors including (but not necessarily limited to) age, body size, condition, time of day, and season (Kooyman 1968; Kooyman et al. 1980, 1983; Castellini et al. 1992; Burns and Castellini 1996; Burns and Testa 1997; Burns et al. 1997). Young Weddell seal pups begin to dive and swim within 2 weeks of birth, and from then until weaning at 6 weeks of age their diving skills and ability are determined mainly by their age (Kooyman 1968; Burns and Castellini 1996; Burns and Testa 1997b). This strong ontogentic component may be a result of the immature physiological status at birth: nursing pups are unable to control their heart rate, respiration, and metabolism to the same degree as older pups, yearlings, or adults (Elsner et al. 1977; Kooyman et al. 1980, 1983; Burns and Castellini

1996; Zenteno-Savin 1997). However, by the time Weddell seals are 1 year old, they have matured physiologically, and their behavioral patterns appear to be determined more by body size and condition than by age (Burns et al. 1997). How and when the diving behavior of Weddell seal pups switches from being determined mainly by age to being influenced by mass and other environmental factors is not clear at this time.

Understanding the factors that influence the successful development of diving skills is particularly important because such research may shed light on patterns of dispersal and recruitment. Weddell seal pups born in Erebus Bay leave McMurdo Sound soon after weaning, and are often never seen again (Kooyman 1968; Stirling 1969; Burns 1997; Testa 1987). Fewer than 25% of the pups born in Erebus Bay are recruited into the breeding adult population (Testa 1987; Hastings 1996). While the annual movements and dispersal patterns of resident females have been documented (Testa 1994), the routes followed by dispersing pups have not been studied. However, it has been hypothesized that after pups leave the breeding colonies they utilize pack ice and the Antarctic coastline as a refuge from competition and predation (Smith 1965; Stirling 1969).

Given the extensive information available on the behavior and physiology of Weddell seals during the summer months, the absence of data on pup behavior during their first, critical winter is especially noticeable. What little information that does exist suggests that, as is the case in other pinnipeds, juvenile dive behavior continues to develop throughout the winter as pups grow and mature (Lydersen et al. 1994; Thorson and Le Boeuf 1994; Le Boeuf et al. 1996; Burns and Testa 1997; Burns et al. 1997; Horning and Trillmich 1997; Stewart 1997). In addition, data collected from adults during the fall and winter suggests that pup behavior may be substantially different from that seen in the summer due to changes in ice conditions and light levels (Kooyman 1975; Castellini et al. 1992; Testa 1994). In order to identify some of the factors that may influence the diving behavior of Weddell seal pups, and to identify emigration and dispersal routes, we tagged young pups with satellite-linked time-depth recorders (SLTDRs) designed to collect and transmit information on both diving behavior and animal location for up to 1 year. From the data collected we hoped to determine: (1) how pup dive behavior changed throughout the winter, (2) if factors such as age, season, time of day, and location influenced dive behavior, and (3) where pups went when they left their natal area.

Materials and methods

Animal handling

Over the austral summers of 1992, 1993, and 1994, in Erebus Bay, McMurdo Sound, Antarctica, 26 weaned Weddell seal pups (11 females, 15 males) were outfitted with 0.5-W SLTDRs (Wildlife Computers, Mark 3.x). Pups were manually restrained and the SLTDRs were attached to their fur with epoxy (Burns and Testa 1997). Tags were designed to be carried by the animal for the next 9 months. At the time the SLTDRs were attached pup age, as determined from tagging records, ranged from 5 to 15 weeks, and mass ranged from 72.0 to 136.5 kg (Table 1). Only data from weaned pups are reported in this study. Pups were not weighed again after the tags were deployed.

Dive data

The SLTDR tags deployed transmitted the number of dives in each of six depth and duration 'bins' for each of four, 6 h periods of the day. The tags had a depth resolution of ± 2.0 m, with a maximum depth of 498 m, and a sampling frequency of 10 s. Depth bins were set as follows: 12–80 m, 81–160 m, 161–240 m, 241–320 m, 321–400 m, and greater than 400 m. Five duration bins each had a range of 4 min, and the sixth recorded all dives of longer than 20 min. Periods were set as 2100–0259 hours (night), 0300–0859 hours (morning), 0900–1459 hours (afternoon), and 1500–2059 hours (evening) local time (GMT + 12 h). The summarized depth and duration data for each of the previous four periods was transmitted as often as possible, provided transmission criteria were met (Burns 1997). Seal positions were determined by the Argos system, provided that the message reception met the criteria set by Service Argos (Hill 1993; Service Argos 1996).

Transmitted data received by Service Argos were retrieved and analyzed using programs supplied by Wildlife Computers (SatPak 3.0). The number of dives in each depth and duration bin, the total number of dives, the date and period of data collection, and the status (on land, or at sea) of the tag were determined for each record. The maximum dive depth within each 24 h period was determined from separate status messages (Burns 1997). The proportion of dives in each bin was determined for each record, provided that the total number of dives was greater than zero. In those cases where the total number of dives was zero, the proportion of dives in all bins was also set to zero. Seal age (in weeks) was then added to the data file, and the mean proportion of dives in each bin was calculated for each seal at each age and period. The median number of days from which data were received for each seal at each age and period was 3 [mean (SD) 2.8 (1.6)]. To control for a different number of data points within each mean value, individual means were weighted by the number of days from which data were received in all subsequent statistical tests. Mean dive frequency (the average total number of dives in each period) was determined for each seal at each age, as was mean maximum dive depth.

The effects of seal age and/or period of day on dive behavior (proportion of dives, mean frequency, and maximum depth) were tested using parametric statistics, provided that the data were normally distributed and there were data from more than five seals in any given period and bin. Data normality was assessed using rankit plots and the Wilk-Shapiro (W-S) statistic (normality accepted if W-S > 0.90), and outliers were visually identified and removed (Shapiro and Wilk 1965). All proportional data were arcsin transformed in order to achieve normality.

Linear regression was used to model the effect of age on the dive parameters of interest separately for each period. The mean values for individual seals at each age were weighted for the number of days in the week for which data were available and then averaged to produce an overall mean for all seals at each week age. Regression equations and mean values were then calculated from these grand means, after weighting for the number of individuals seals which contributed to the grand mean. Regression equations were reported provided that $P < 0.05$ and that seal age accounted for more than 10% of the overall variation in dive behavior within any given period. In those periods where seal age did not have a significant effect on dive behavior, the mean dive behavior, for all ages pooled, was determined for each animal. One-way analysis of variance (ANOVA) methods were then used to test for differences among periods in these overall mean dive parameters.

Table 1 Satellite tag deployment history. Satellite-linked time-depth recorders (SLTDRs) with identification numbers 92-x were version 3.04, while tags 93-x were version 3.1. The seal identification (ID) starts with an *M* for male pups, and an *F* for females. The age and mass of the seal (weeks/kg) at the time of deployment is indicated in parentheses below the ID number. Dates indicate the range of transmission dates, rather than when tags were deployed and recovered

SLTDR	1992–93 Seal ID	Dates	SLTDR	1993–94 Seal ID	Dates	SLTDR	1994–95 Seal ID	Dates
92–419	M10082 (17/106.4)	2/6–7/24[c]	92–417	F10691 (9/99.8)	12/28[a,b]	92–417	M11022 (5/98.0)	12/01–1/01
92–418	M10297 (15/112.3)	2/7–4/22	92–419	M10524 (11/92.8)	1/6–3/10	92–425	F10968 (6/131.6)	12/01–12/10
92–420	F10253 (13/90.8)	2/1–5/2	92–426	F10768 (8/116.2)	12/26[a,b]	93–223	M10954 (7/123.7)	12/04–12/24[b]
92–421	M10092 (16/84.9)	2/8–5/27	92–425	M10475 (8/118.1)	12/14–1/7[b]	93–224	F10952 (7/114.7)	12/07–1/10
92–422	F10145 (12/93.7)	1/13–2/17	93–223	M10531 (7/95.8)	12/12–1/5[b]	93–225	M11021 (5/103.1)	12/02–12/27
92–423	M10140 (11/91.4)	1/10–5/15	93–224	M10549 (6/106.7)	12/5–1/6[b]	93–229	F10951 (6/106.0)	11/24–12/15[b]
92–424	M10141 (13/72.0)	1/22–3/13	93–225	M10717 (5/113.8)	12/6–12/27[b]	93–266	F10967 (5/136.5)	11/29–12/10
			93–226	F10533 (7/104.6)	12/12–4/2			
			93–227	M10481 (6/106.0)	11/30–1/16			
			93–229	F10718 (6/133.0)	12/13–1/13[b]			
			93–230	F10869 (5/81.3)	12/14–2/22			
			93–266	M10767 (6/116.0)	12/14–2/4[b]			

[a] Tag failed upon deployment due to technical error and was retrieved
[b] Tag retrieved after broken antenna detected
[c] Tag retrieved in the subsequent season

Location data

Seal positions were calculated by the Argos system based on the Doppler shift in transmitted signals, provided that a sufficient number of signals was received during the satellite overpass. When an insufficient number of signals was received, dive data, but no location data, were received (Fancy et al. 1988, Service Argos 1996). The accuracy of the locations calculated by Argos varies with the number of signals received during a satellite pass, and is reflected in the quality ranking of the location (called the location class or LC). To account for differences in LC, all location data were screened for outliers before animal locations and movement rates were calculated.

To remove inaccurate locations, we used a three-step process (Frost and Lowry 1994; Frost et al. 1995). First, all positions with a LC rank of < −5 were discarded. These locations were calculated by Argos using fewer than two signals, and were generally unreliable. Secondly, the Keating error index (KEI) value was calculated for each record, and all records with a KEI > 20 and a LC < 1 were omitted. The KEI identifies erroneous locations by taking into account the time and distance between sequential positions and assuming that any single, relatively large distance movement that is followed shortly thereafter by a return to the original position is an error (Keating 1994). The records were then screened for improbable locations given the time and distance between sequential positions, and the maximum swimming speed of the seals (as per Frost and Lowry 1994; Frost et al. 1995). Following the removal of these records, the KEI was recalculated, and all records with a KEI > 20 were omitted. Before any locations marked for deletion were permanently removed from the dataset, they were carefully rechecked to verify that they were actual outliers. Only those positions that remained after this process were used to track Weddell seal movements. Since LC codes of 2 or less had an estimated error of > 5 km (Burns and Castellini in press), it was possible to have "good" locations that placed seals on land. These data were retained in all analyses.

Once a database of all reasonable locations was compiled, daily positions were estimated for each seal by averaging all positions received during each day. Daily movement rates were then determined by calculating the distance between two subsequent daily positions, and dividing by the number of days between the locations. For each seal the average daily movement rates for each month was computed. This value was then weighted by the number of datapoints, and the mean monthly movement rate within each of five regions within the Ross Sea was then calculated for all seals combined. Comparisons of movement rates between regions and months were made using a one way ANOVA.

Finally, seal locations were used to identify dispersal routes, and to determine the effect of location (region) on dive behavior. However, because seal locations were determined separately from dive behavior, there were far fewer days with good positions than days with dive records. Therefore, in order to assign a position to all dive records, animals were assumed to remain within a region until they were located outside that region.

Results

Tag performance

Among the 26 pups outfitted with SLTDRs during the course of this study, there was a high tag failure rate, and no tag transmitted for longer than 5.5 months. Three tags failed immediately upon deployment for unknown reasons, and during the 1994 and 1995 seasons ten tags

were retrieved within 6 weeks of deployment with missing or broken antennase (Table 1). Only one tag transmitted after May of the following year. Despite these problems, a total of 1459 depth, 1481 duration, and 204 maximum dive depth records were received from 23 seals of between 8 and 27 weeks of age. However, data reception was sporadic. The median number of days within each week from which data were received was 3, and only 15% of the records (for a given seal, age, and period) contained more than 4 days of data per week.

Dive depth

There were dives in all six depth bins (to 400 + m), and the maximum dive depth was 678 m for a 12-week-old pup. Approximately half of all dives made by pups were to depths less than 80 m, and one quarter of dives were to depths between 80 and 160 m. The effect of age was highly variable: overall age effects were rare, but at times, age accounted for more than 60% of the variation in the proportion of dives within each bin (Table 2). While time of day did influence dive behavior, the effect varied by period and depth. For example, the proportion of dives shallower than 160 m decreased with age in the afternoon period, but remained constant with age in all other periods. Age had no effect on the proportion of dives within any depth range in the night or morning periods, or any impact on the proportion of dives deeper than 400 m (bin 6). However, the proportion of dives in depth bins 4 and 5 (241–320 and 321–400 m) increased significantly with age in both the afternoon and evening periods (r^2 = 45–78%; Fig. 1, Table 2). The average maximum depth of dives made by individual seals increased significantly as seals aged, but age accounted for only one third of the overall variance (mean maximum depth = 198.45 + 6.39 ∗ Age, $n = 20$, $r^2 = 0.20$, $P = 0.03$; overall mean 304.41 ± 14.91 SE).

Dive duration

One-third of all pup dives had a duration of less than 4 min, and half were between 4 and 8 min. There were no dives in duration bins 5 or 6, which indicated a maximum dive duration of no greater than 16 min. Age effects were only evident in the night and afternoon periods, and age never accounted for more than half of the variation in dive duration. Age effects were evident in duration bins 1, 3, and 4 (0–4, 8–12, and 12–16 min, respectively Table 3). The proportion of short dives (bin 1, 0–4 min) decreased with age in the afternoon period, but remained constant with age in all other periods. In contrast, the proportion of dives of between 8 and 16 min increased with age in the afternoon period, but decreased with age in the night period. In excess of 40% of dives made by older pups in the afternoon were longer than 8 min. In the remaining periods, long dives accounted for fewer than 20% of the total dives, and age had little effect (Fig. 2).

Dive frequency

Both age and time of day had a significant impact on mean dive frequency. While there was no effect of age on

Table 2 The effect of age and period on the mean proportion (± SE) of dives in the different depth bins. Reading across the table, similar letter codes indicate that the mean proportion of dives did not differ significantly among periods within that bin [one-way analysis of variance (ANOVA), post-hoc comparison of means, $P > 0.05$]. Comparisons were not made between bins within the same period. Significant increases (+ AGE) or decreases (−AGE) in the proportion of dives within each bin and period are indicated, and regression equations provided

Depth bin	Night (21:00–02:59) $n = 20$	Morning (03:00–08:59) $n = 20$	Afternoon (09:00–14:59) $n = 20$	Evening (15:00–20:59) $n = 20$
1: 12–80 m	63.93 ± 3.10 A	54.00 ± 2.18 B	−Age[1]	46.92 ± 3.47 B
2: 81–160 m	27.10 ± 2.16 C	27.25 ± 1.17 C	−Age[2]	27.05 ± 1.75 C
3: 161–240 m	6.46 ± 1.22 D	13.20 ± 1.23 E	14.62 ± 1.59 E	16.72 ± 2.03 E
4: 241–320 m	1.55 ± 0.49 F	4.36 ± 0.67 G	+ AGE[3]	+ AGE[5]
5: 320–400 m	0.79 ± 0.38 H	0.84 ± 0.25 H	+ AGE[4]	+ AGE[6]
6: 400 + m	0.16 ± 0.06 I	0.35 ± 0.11 I	1.48 ± 0.66 J	0.83 ± 0.40 I

[1] $Y = 1.09 - 0.0213 \times Age$, $r^2 = 0.46$, $P = 0.0004$
[2] $Y = 0.67 - 0.0123 \times Age$, $r^2 = 0.42$, $P = 0.0009$
[3] $Y = -0.17 + 0.0277 \times Age$, $r^2 = 0.78$, $P < 0.0001$
[4] $Y = -0.12 + 0.0187 \times Age$, $r^2 = 0.45$, $P = 0.0005$
[5] $Y = -0.04 + 0.0167 \times Age$, $r^2 = 0.66$, $P < 0.0001$
[6] $Y = -0.11 + 0.012 \times Age$, $r^2 = 0.67$, $P < 0.0001$
In all cases $Y = arcsin$ (*mean proportion*$^{1/2}$)

Fig. 1 The mean proportion of dives within each of the six depth bins for each of the four periods of the day

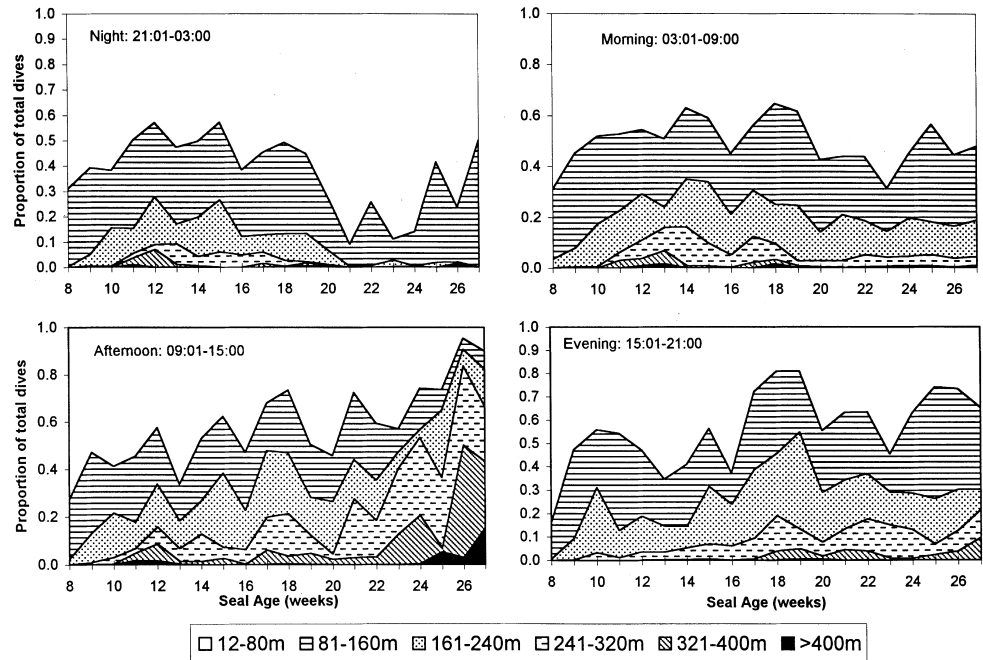Legend: □ 12–80m ⊟ 81–160m ▨ 161–240m ▱ 241–320m ▨ 321–400m ■ >400m

Table 3 The effect of age and period on the mean proportion (±SE) of dives in the different duration bins. Reading across the table, similar letter codes indicate that the mean proportion of dives did not differ significantly within the same bin among periods (one-way ANOVA, post-hoc comparison of means, $P > 0.05$). Comparisons were not made between bins within the same period. Significant increases (+AGE) or decreases (−AGE) in the proportion of dives within each bin and period are indicated, and regression equations provided

Duration bin	Night (21:00–02:59) $n = 20$	Morning (03:00–08:59) $n = 20$	Afternoon (09:00–14:59) $n = 20$	Evening (15:00–20:59) $n = 20$
1: 0–4 min	48.92 ± 3.16 A	38.79 ± 2.54 A,B	−AGE[2]	34.08 ± 2.72 B
2: 4–8 min	42.99 ± 2.92 C,D	48.80 ± 3.15 D	39.86 ± 3.26 C	53.14 ± 2.36 D
3: 8–12 min	−AGE[1]	12.02 ± 1.45 E	+AGE3	12.31 ± 1.18 E
4: 12–16 min	0.49 ± 0.19 F	0.36 ± 0.10 F	+AGE4	0.39 ± 0.14 F

[1] $Y = 0.457 - 0.012 \times Age$, $r^2 = 0.30$, $P = 0.006$
[2] $Y = 0.968 - 0.018 \times Age$, $r^2 = 0.48$, $P < 0.0003$
[3] $Y = 0.076 + 0.021 \times Age$, $r^2 = 0.40$, $P = 0.0012$
[4] $Y = -0.053 + 0.007 \times Age$, $r^2 = 0.21$, $P = 0.0205$
In all cases, $Y = $ arcsin (mean proportion$^{1/2}$)

the number of dives in the afternoon period, dive frequency (mean no. of dives/period) increased significantly with age in the morning, evening, and night periods (morning dive frequency $= 16.82 + 1.08* $ age, $r^2 = 0.44$, $P = 0.0008$; evening dive frequency $= 3.11 + 1.42*$ age, $r^2 = 0.63$, $P < 0.0001$; night dive frequency $= 14.83 + 1.36*$ age, $r^2 = 0.50$, $P = 0.0003$). In these three periods, dive frequency increased from an average of 19.5 ± 4.2 (SE) dives/period for 8-week-old seals, to 39.4 ± 2.4 dives/period for 27-week-old seals. In contrast, pups of all ages made an average of 24.8 ± 1.0 dives in the afternoon period (Fig. 3). Overall, dive frequency increased from approximately 91 to 164 dives/day as the pups' age increased.

Location data

Of the 1071 original locations received, 559 (52.2%) were discarded in the screening process. Of the remaining locations, 54.9% were LC 0 or lower, 41.8% were LC 1, and 2.9% LC 2. Overall, 67.8% of the locations received from tags on ice were of LC 1 or better, but only 30.5% of locations received from tags at sea were of similar quality. The estimated accuracy of these locations is 11.35 ± 1.67 km for LC 0 or lower, and 5.03 ± 1.17 km for LC 1. The accuracy of LC 2 positions was not estimated because of the small number of LC 2 position fixes received (Burns and Castellini, in press).

Fig. 2 The mean proportion of dives within each of the four duration bins for each of the four periods of the day
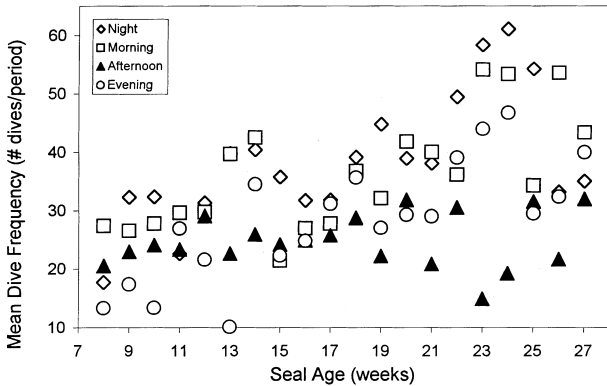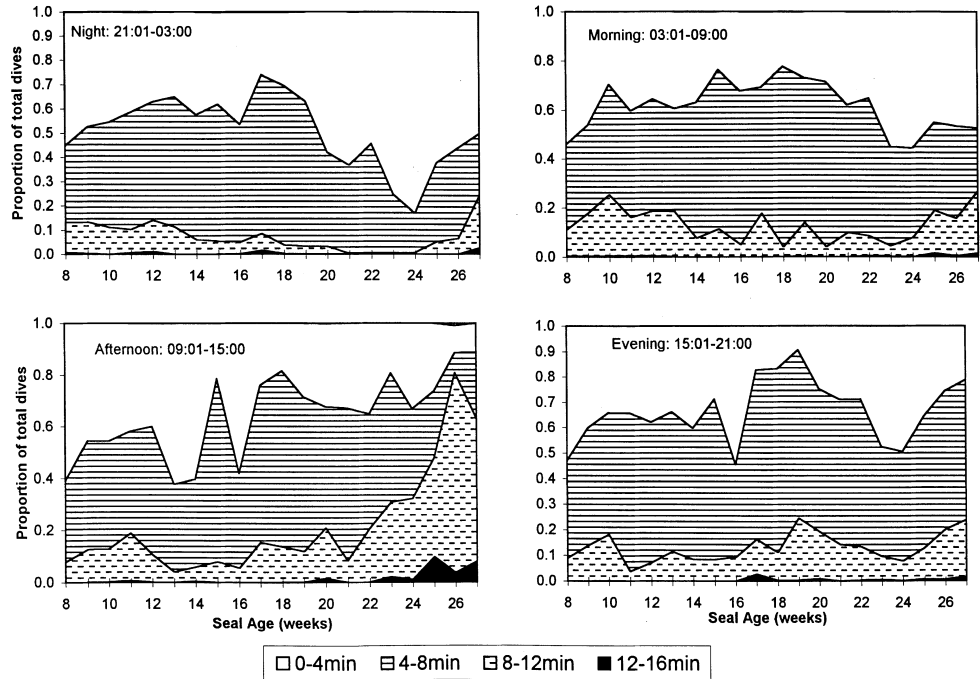

Fig. 3 The mean number of dives in each period of the day for seals between the ages of 8 and 27 weeks. The mean dive frequency increased significantly with age in the morning, evening, and night periods, but did not change with age in the afternoon

The location data received ($n = 512$) indicated that the majority of pups stayed within the greater Erebus Bay region during the months of November, December, and January (Fig. 4). Since all 1994 tags had failed by the end of January, all positions calculated for seals in 1994–1995 were within this region. Satellite records exist for ten seals in February (three from 1993, and seven from 1992). Of these seals, four remained in Erebus Bay during February, while the remaining animals began to move out of Erebus Bay and towards the coastline of the Antarctic continent. Four animals traveled northwest up the coast, while two traveled southwest out of Erebus Bay (Fig. 5).

In March of 1993 and 1994, transmissions were received from seven seals, of which only two remained within Erebus Bay for the entire month. All other seals moved north along the coastline (Fig. 6). Seal 10253 traveled the furthest, and by the end of March had moved over 400 km from Erebus Bay. By the middle of April, three of the seals that had traveled north out of Erebus Bay returned. However, two other seals did not return. Seal 10253 continued to move north along the Antarctic coast and by the end of April was near Cape Adare, over 700 km from Erebus Bay. The other seal (10092) stopped moving north after reaching the Drygalski Ice Tongue, approximately 350 km from Erebus Bay. Transmissions were received from only one animal after the end of May, and this animal (10082) appeared to remain in the north McMurdo Sound region (Fig. 7).

Average rates of travel (km/day) differed by month, with December having the lowest rate of travel (5.2 ± 0.9 km/day) and March the greatest (16.7 ± 2.9 km/day) (one-way ANOVA, $F_{5,70} = 4.19$, $P = 0.0024$, Tukey post-hoc comparison of means, $P < 0.05$; Table 4). All movement rates were based on the average daily positions and do not necessarily indicate that the seals were moving in a directed fashion. When compared by region, movement rates within Erebus Bay were significantly lower than those outside the region (one-way ANOVA, $F_{4,70} = 7.28$, $P = 0.001$, Tukey post-hoc comparison of means, $P < 0.05$; Table 4). There were some differences in the diving behavior of pups in the different regions of the Ross Sea (one-way ANOVA), but not all regions were different from each other ($P < 0.05$ post-hoc comparison of means). Seals in Erebus Bay made the most short and shallow dives, while mid-depth and duration dives predominated in the McMurdo Sound regions. Diving behavior in the Ross Sea and along the Antarctic coast were similar (Table 5).

Fig. 4 Average daily locations in November, December, and January for pups tagged in 1992, 1993, and 1994. The letters, numbers and symbols in the key stand for individual seal pups, which are referenced by their ID numbers
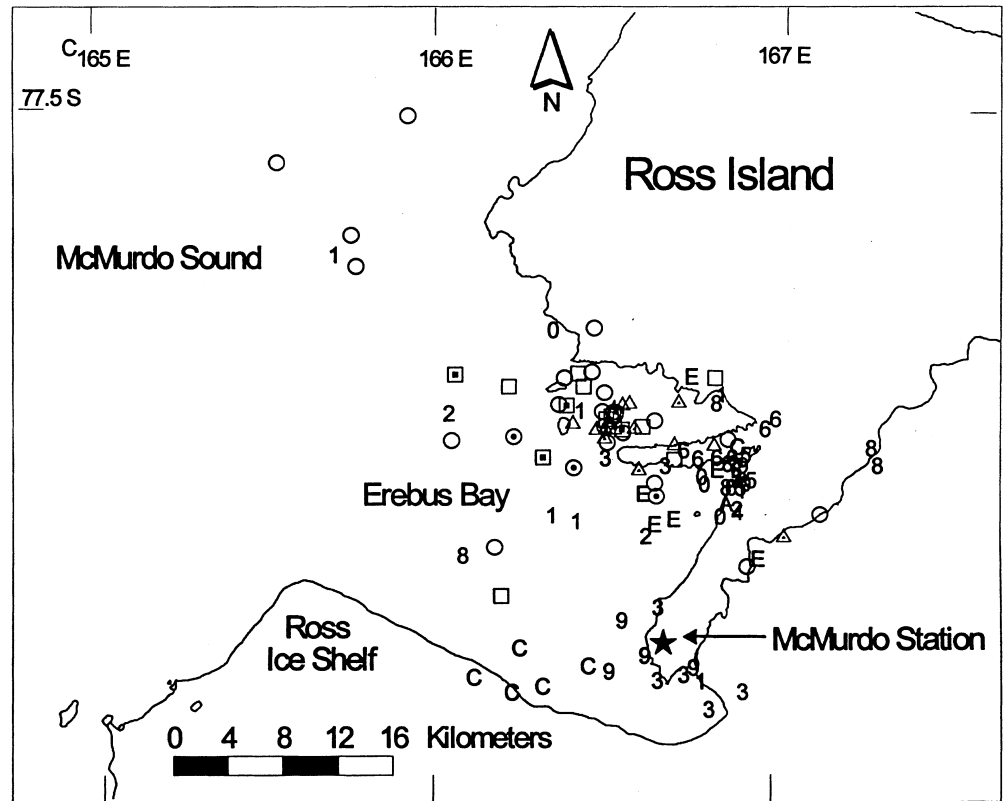
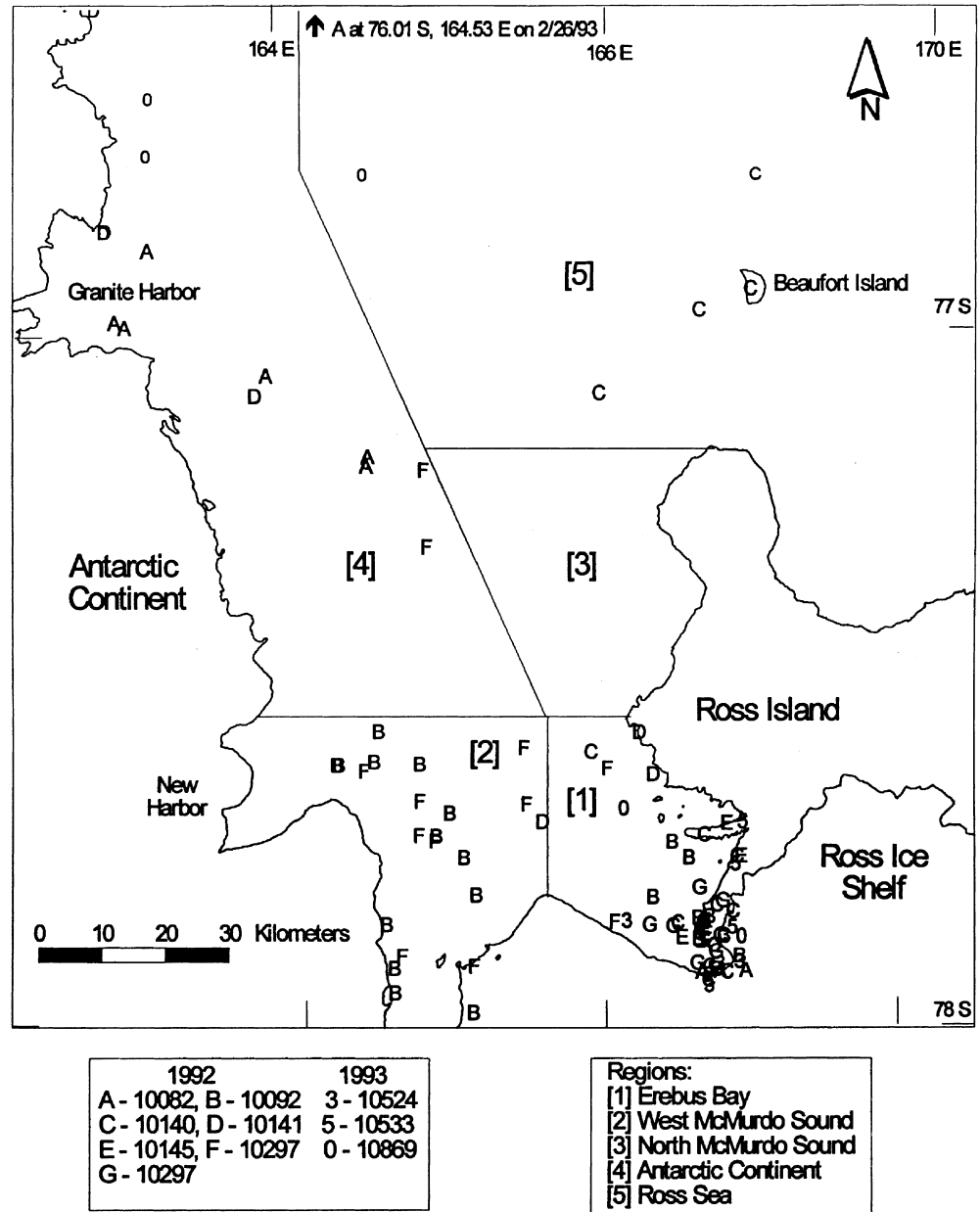|	1992	1993	1994	
	A - 10082, B - 10092	1 -10475, 2 - 10481	□ - 10951,	○ - 10952
	C - 10140, D - 10141	3 - 10524, 4 - 10531	△ - 10954,	▣ - 10967
	E - 10145, F - 10253	5 - 10533, 6 - 10549	⊙ - 10968,	△ - 11021
	G - 10297	7 - 10717, 8 - 10718		
		9 - 10767, 0 - 10869		

Discussion

Diving behavior

While studies on very young pups have indicated that age accounts for between one-half and three-quarters of the variation in dive behavior throughout the day (Burns and Testa 1997), the effect of age on the diving ability of Weddell seals between the ages of 2 and 7 months was far less predominant. In fact, age effects were only evident for changes in the proportion of deep and long dives in the afternoon and evening periods, and in mean dive frequency during all but the afternoon period. The absence of positive age effects on dives shorter than 8 min and shallower than 160 m was not unexpected given that these dives are well within the diving capability of newly weaned Weddell seal pups (Burns and Castellini 1996, Burns and Testa 1997). It was surprising, however, that strong correlations between age and deeper and longer dives were absent in all but the afternoon period.

While it is likely that the size of the bins (4 min, 80 m) obscured some shifts in mean dive depth and duration

because bin ranges were large relative to the expected changes in mean parameters, bin midpoints are unbiased estimators of mean dive parameters for pups of up to 13 weeks of age (Burns and Castellini, in press). This suggests that for the younger pups in this study, bin ranges were not obscuring behavioral changes, and the general absence of age effects was not an artifact of the sampling regime. It appears that while changes in young pup dive ability are driven by the maturation of physiological control mechanisms (Burns and Castellini 1996), slower changes in mass and body condition in post-weaned pups drive the more gradual increases in the dive ability seen here (Rea 1995; Burns 1997). Similar shifts in the importance of age and mass has also been seen in the diving patterns of juvenile northern elephant seals and Galapagos fur seals (Thorson and Le Boeuf 1994; Le Boeuf et al. 1996; Horning and Trillmich 1997). Unfortunately, because animals were not weighed after tag deployment, it is not possible in this study to tease apart the effects of age and mass.

In contrast to dive depth and duration, mean dive frequency was generally positively correlated with age. Combined dive depth and duration data suggest that Weddell seal pups were attempting to maximize dive

Fig. 5 Average daily locations in February for pups tagged in 1992 and 1993. The five regions within the Ross Sea used for grouping animal locations, dive behavior and movement rates are also shown. The letters and numbers indicate individual seal pups originally tagged in 1992 & 1993, as in Fig 4


	1992	1993
	A - 10082, B - 10092	3 - 10524
	C - 10140, D - 10141	5 - 10533
	E - 10145, F - 10297	0 - 10869
	G - 10297	

Regions:
[1] Erebus Bay
[2] West McMurdo Sound
[3] North McMurdo Sound
[4] Antarctic Continent
[5] Ross Sea

time, but that the manner in which this was done changed with age and time of day. In those periods where dive frequency increased with age, the mean proportion of dives in each depth and duration bin remained fairly constant, whereas in the afternoon period dive frequency remained constant but the proportion of deep and long dives increased with age. In combination, as animals aged, they made more dives, and made proportionally more deep and long dives. That seals did not increase their dive frequency in the afternoon as the dive depth and duration increased suggests that dive frequency may be constrained by limits on the total time Weddell seal pups can spend diving. That dive frequency did not decrease as dive depth and duration increased in the afternoon further suggests that this limitation was due to physiological or behavioral factors rather than a

close coupling between dive frequency, depth, and duration, as has been seen in other diving vertebrates.

The absence of a strong correlation between dive frequency and duration is likely to be a result of the fact that seals did not spend all of their time diving. The average amount of time pups spent below 12 m never exceeded three out of six available hours, and in the afternoon period, when the proportion of long dives increased, the total time underwater averaged less than 2.5 h per period (Burns 1997). These estimates of time spent underwater are necessarily rough, and do not include the time seals spent in the water near the surface. Nevertheless, they do suggest that the deep and long dives made by pups are physiologically more expensive than shorter dives, and that as the proportion of these dives increases, the time animals must spend at the

Fig. 6 Average daily locations in March for pups tagged in 1992 and 1993. Individual seals are keyed as in figs 4 and 5
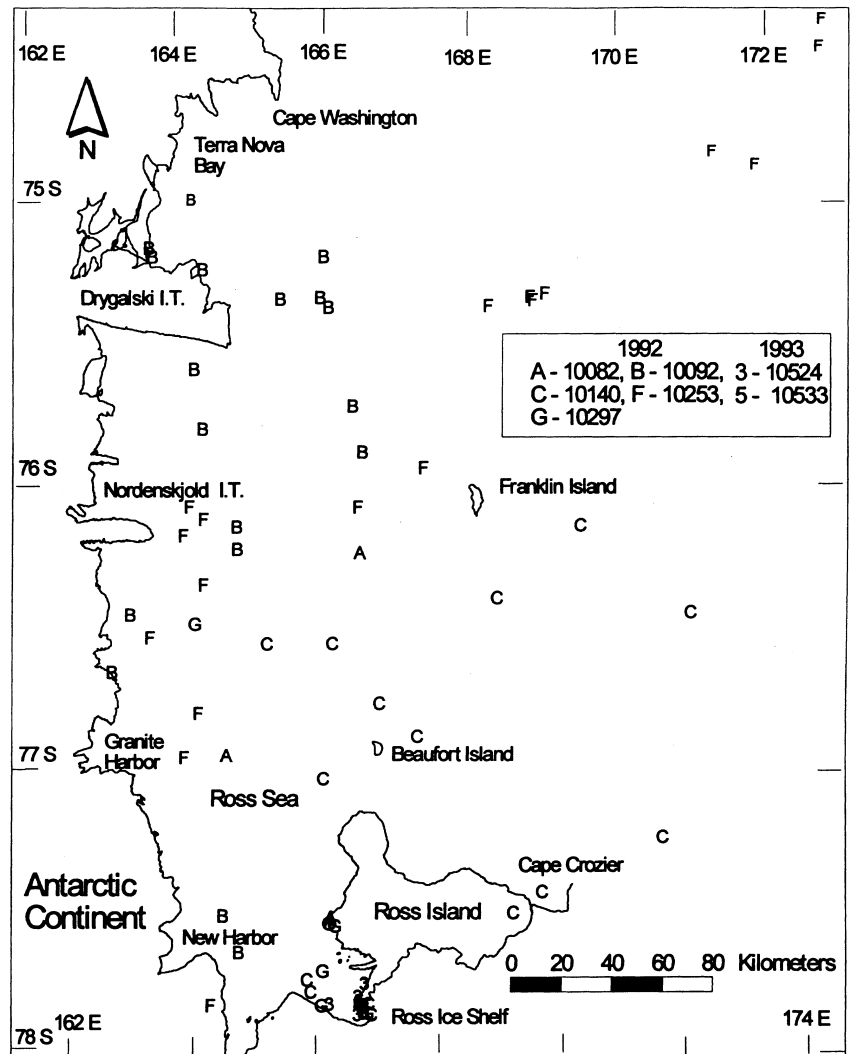
surface in recovery increases. Given that the aerobic dive limit (as determined from post-dive lactate samples) of 6 week-old Weddell seal pups is approximately 6 min, and that of yearlings is between 10 and 14 min, it is likely that the long and deep dives made by pups during the afternoon period include anaerobic dives that require increased surface recovery periods (Kooyman et al. 1980, 1983, Burns and Castellini 1996). As such recovery periods would effectively reduce the total time spent underwater, and presumably the time available for foraging, pups may be adjusting the frequency, depth and duration of dives in response to both their physiological limitations and their need to make deep and long dives in order to obtain prey. Such tradeoffs between dive frequency, depth, and duration have been frequently hypothesized but less often observed in the field (Fedak et al. 1988; Ydenberg and Clark 1989; Houston and Carbone 1992; Fedak and Thompson 1993).

The effect of time of day, and the shift in the importance of deep and long afternoon dives, resembles the pattern seen in adult female Weddell seals and other Antarctic divers that forage on vertically migrating species (Croxall et al. 1985; Bengtson and Stewart 1992; Boyd and Croxall 1992; Castellini et al. 1992; Wilson et al. 1993; Testa 1994). This suggests that foraging Weddell seal pups may make deep and long dives in the afternoon in order to obtain prey, but are able to concentrate their efforts in shallower waters during the rest of the day. However, directly relating dive behavior to prey abundance or light levels during the different periods is complicated by the extreme changes in daylight patterns that occur in the region, and the absence of information on the ecology and distribution of Weddell seal prey items under fast ice and within the Ross Sea. In McMurdo Sound, light levels are relatively high and constant until the end of February, and relatively low and constant from late April through to the end of this study (first sunset 23 February, last sunrise 23 April, Kooyman 1975; Castellini et al. 1992). The changes in ambient light level suggest that vertically migrating prey are found closer to the surface during autumn and winter afternoons, when light levels are much lower than during the summer months. However, two findings indicate that diel variation in light levels did not *solely*
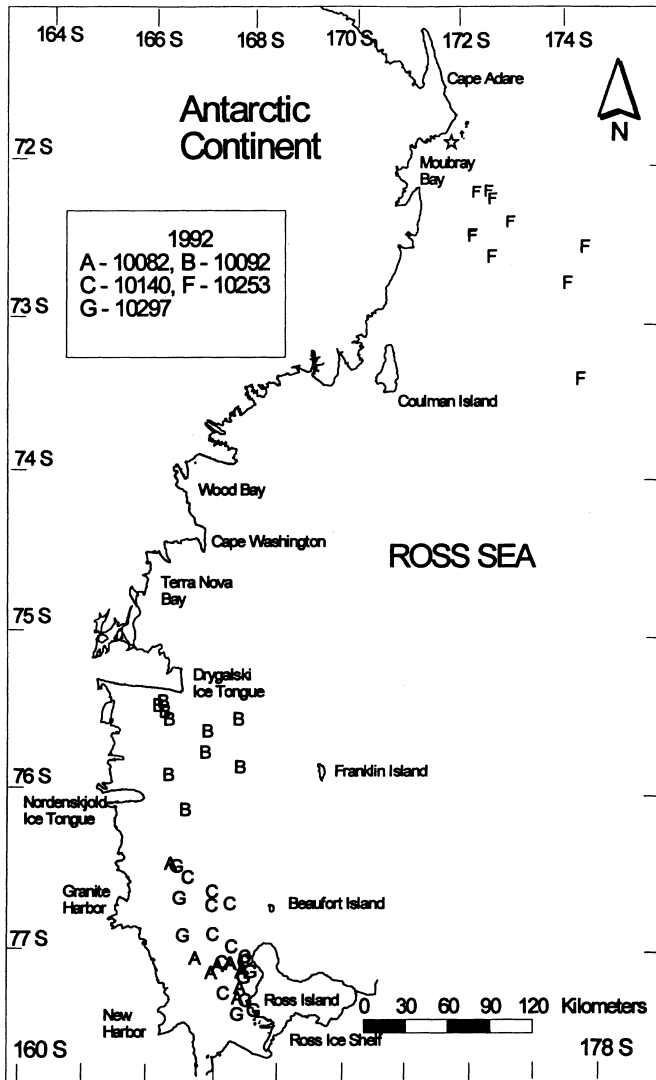
Fig. 7 Average daily locations in April and May for pups tagged in 1992. Seals are keyed as in Figs 4–6

determine dive behavior: first, mean dive depth continued to increase during the afternoon period, even once the sun had ceased to rise; and second, dive depths did not become shallower as the season progressed, as should have been the case were dives and prey strictly tracking ambient light levels.

It may be that Weddell seal prey items do not make extensive vertical migrations when under the fast and pack ice of McMurdo Sound, especially when light levels are low. While studies of the major prey groups have indicated that most of the prey selected by Weddells occur midwater, are separated in size by depth, or make diurnal vertical migrations, this work has been exclusively carried out during the summer in ice-free antarctic waters around the Antarctic Penninsula. No data on prey movements or distribution are available from McMurdo Sound or from any season other than mid summer (Hubold 1984; Eastman 1985; Kellermann 1986; Ekau 1990; Rodhouse 1990; White and Piatkowski 1993). In McMurdo Sound, the principal prey for adults throughout the year appears to be the antarctic silverfish (*Pleuragramma antarcticum* Boulanger), a small (< 15 cm) fish that is most often found between the depths of 100 and 350 m (Dearborn 1965; Hubold 1984; Eastman 1985; Green and Burton 1987; Castellini et al. 1992; White and Piatkowski 1993; Burns et al. 1998). Foraging adults and yearlings concentrate their dives in this depth range throughout the day and year. Diel variation in dive depth and duration, while evident in some adult dive records from the autumn months, was largely absent from most adult and yearling summer and winter dive records (Castellini et al. 1992; Testa 1994; Burns and Testa 1997; Burns et al. 1997). Since approximately one-third of the dives made by pups in this study fell between 80 and 320 m, and scats collected within Erebus Bay contained predominantly fish bones and small squid beaks, it is likely that newly weaned Weddell seal pups are also forage on *Pleuragramma* and

Table 4 Average movement rates (km/day ± SE) calculated for seals in different months and in different regions of the Ross Sea. NSD (not significantly different) indicates that fewer than four seals were located in that region during the month. Sample sizes are the number of individual seals located within all regions for the given month. (*W.* west, *N.* north)

Month	Erebus Bay	W. McMurdo Sound	N. McMurdo Sound	Antarctic Coast	Central Ross Sea	Overall
December (n = 13)	6.0 ± 0.6	–	–	–	–	5.2 ± 0.9
January (n = 9)	5.7 ± 0.8	–	–	–	–	5.3 ± 1.2
February (n = 19)	5.0 ± 0.8	NSD	NSD	17.8 ± 5.2	NSD	10.5 ± 2.1**
March (n = 16)	5.8 ± 2.0	NSD	23.8 ± 12.2	18.6 ± 3.1	22.1 ± 2.4	16.7 ± 2.9**
April (n = 9)	NSD	NSD	NSD	9.2 ± 4.0	14.2 ± 4.9	11.6 ± 2.1**
May (n = 5)	–	–	NSD	NSD	NSD	5.9 ± 2.3
Overall	5.3 ± 0.6*	13.2 ± 0.9	15.6 ± 5.5	15.4 ± 2.4	14.8 ± 2.8	10.1 ± 1.1

*Movement rate in Erebus Bay significantly less than that in all other regions (all months grouped) $P < 0.05$
**Movement rates significantly elevated over remaining months (all regions combined), $P < 0.05$
Tukey (HSD) post-hoc comparison of means

Table 5 The mean ($\pm$SE) proportion of dives in each bin for all seals diving in each region. Significant differences among the regions in the proportion of dives within each bin are indicated by a $\uparrow$ for regions with higher than average proportion of dives within that bin, and a $\downarrow$ for regions with a significantly lower than average proportion (one-way ANOVA, Tukey post-hoc comparison of means, $P < 0.05$). Sample sizes are the number of records within each region, with each record a separate seal and week age

	Erebus Bay	W. McMurdo Sound	N. McMurdo Sound	Antarctic Coast	Central Ross Sea
$n =$	102	6	11	20	28
Bin 1					
12–80 m	58.7 $\pm$ 2.3$\uparrow$	34.6 $\pm$ 11.6	35.4 $\pm$ 8.8	42.2 $\pm$ 5.3	47.8 $\pm$ 4.1
1–4 min	41.8 $\pm$ 1.8	25.9 $\pm$ 7.6	33.3 $\pm$ 8.5	27.9 $\pm$ 5.4	41.1 $\pm$ 4.5
Bin 2					
81–160 m	25.8 $\pm$ 0.8	36.9 $\pm$ 3.6	27.6 $\pm$ 3.7	31.6 $\pm$ 2.1	26.4 $\pm$ 1.6
4–8 min	46.3 $\pm$ 1.0	67.4 $\pm$ 3.7	48.33 $\pm$ 5.4	60.9 $\pm$ 2.5	46.4 $\pm$ 2.1
Bin 3					
161–240 m	10.9 $\pm$ 1.1$\downarrow$	23.5 $\pm$ 5.9$\uparrow$	16.7 $\pm$ 3.8	17.0 $\pm$ 3.2	14.8 $\pm$ 2.0
8–12 min	10.9 $\pm$ 1.0	6.9 $\pm$ 3.5	1439 $\pm$ 5.5	12.4 $\pm$ 2.7	14.9 $\pm$ 2.0
Bin 4					
241–320 m	3.7 $\pm$ 0.6$\downarrow$	8.7 $\pm$ 4.4	10.7 $\pm$ 3.3$\uparrow$	5.8 $\pm$ 1.2	9.5 $\pm$ 1.8
12–16 min	0.5 $\pm$ 0.1	–	0.6 $\pm$ 0.6	1.4 $\pm$ 0.8	0.6 $\pm$ 0.2
Bin 5					
321–400 min	1.3 $\pm$ 0.4	0.6 $\pm$ 0.5	4.9 $\pm$ 2.7	2.4 $\pm$ 1.1	3.0 $\pm$ 1.0
16–20 min	–	–	–	–	–
Bin 6					
400+ m	0.2 $\pm$ 0.1	–	1.6 $\pm$ 1.2$\uparrow$	0.8 $\pm$ 0.5	0.5 $\pm$ 0.3
20+ min	–	–	–	–	–

Depth Bin 1 $F_{4,168} = 5.52$; Bin 2 $F = 1.25$; Bin 3 $F = 3.02$; Bin 4 $F = 5.69$; Bin 5 $F = 2.01$; Bin 6 $F = 2.40$
Duration Bin 1 $F_{4,1266} = 2.70$; Bin 2 $F = 2.81$; Bin 3 $F = 1.13$; Bin 4 $F = 1.37$

other midwater prey items (Kooyman 1968; Thomas and DeMaster 1983; Burns et al. 1998). Thus, while both the diet and dive information suggest that Weddell seal adults, juveniles, and pups forage on similar prey, and that the prey species show some degree of vertical migration throughout the year, there is little direct evidence for either conclusion.

Movement patterns

In addition to information on dive patterns, the SLTDRs provided a large amount of data on the movement patterns of pups from the late summer through to the early winter. Like adults, all pups remained associated with the fast ice of Erebus Bay during the months of November, December and January (Stirling 1969; Testa 1994). However, soon after weaning, pups began to move away from their natal colony, and by February many of the pups had left Erebus Bay and moved into McMurdo Sound. While pup movements away from Erebus Bay were similar to those observed in SLTDR-tagged adult females, pups tended to leave Erebus Bay earlier, to remain closer to the Antarctic coastline, and to utilize the pack-ice habitat less than the adults (Testa 1994). The early movement of pups from Erebus Bay may indicate an attempt by pups to improve foraging success by avoiding the regions of low prey abundance that surround the breeding and molting areas where adults congregate (Testa et al. 1985; Castellini et al. 1992).

The apparent reliance of pups on coastal fast ice during the migration from Erebus Bay may serve two purposes: young seals would be able to continue foraging within shallower coastal areas while at the same time use the fast ice as a refuge against killer whale predation (Smith 1965). Interestingly, those pups that returned to McMurdo Sound did so after the killer whales and most adult Weddell seals had left the area (Mikhalev et al. 1981, Testa 1994). However, some pups used a habitat similar to that selected by the adults. Two pups were found primarily within the pack ice habitat of the open Ross Sea, while three pups remained within Erebus Bay until March/April, as did many adult females (Testa 1994). Therefore, from this study we were unable to determine if the absence of juveniles from within Erebus Bay during the breeding season was a result of competitive exclusion during periods of high population density, or an indication that juvenile Weddell seals favored a different habitat than adults, as has been shown in studies of young elephant seals and harbor seals (Brown and Mate 1983, Thompson 1989, Hastings 1996, Le Boeuf et al. 1996, Stewart 1997).

While not all pups traveled away from Erebus Bay, at least one pup moved more than 700 km to the north, and several pups moved past the small Weddell seal colonies at the Nordenskjold Glacier, Terra Nova Bay, Wood Bay, and Coulman Island (roughly 180, 330, 410, and 500 km from Erebus Bay, respectively). At this time (1998), none of the pups that "permanently" left Erebus Bay have been resighted. However, sighting probabilities are low for Weddell seals of younger than 6 years, and we do not know if these pups have died, been recruited into other colonies, or just not yet returned to McMurdo Sound (Testa 1987, Hastings 1996). While recruitment into other colonies can not be confirmed, the long dis-

tances moved by pups does indicate the potential for gene flow among all colonies along the western coast of the Ross Sea (Stirling 1969; Testa et al. 1985).

In addition to tracking migration patterns, it was also possible to examine dive behavior and average daily movement rates within different regions of the Ross Sea. Overall, the dive behavior in the five regions was remarkably similar, as was the case for adult Weddell seals throughout the winter (Testa 1994). This supports the idea that pups throughout the Ross Sea were foraging on similar prey items, or at least in similar habitats. The similarity of diet among age classes and areas probably reflects the uniformity of the prey base in McMurdo Sound, where *Pleuragramma* makes up more than 90% of the fish biomass (Eastman 1985; Everson 1985). However, the similarity in diving behavior may also be a result of the relatively similar physiological constraints faced by all pups within the study. This is supported by the fact that the few observed differences in diving behavior among regions could generally be attributed to seal age, and were not clearly related to variations in bottom depth or sea-ice conditions. While the shallow inner Erebus Bay region, where young pups were concentrated in December and January, had the highest proportion of shallow and short dives, this probably reflected its use as a natal area, rather than its bathymetry. With the exception of the deeper Ross Sea, the maximum sea-floor depth of all regions is similar and deeper than almost all dives made by the pups, and there was no evidence that pups occasionally shifted to benthic feeding, as has been observed for adult females during the midwinter months (Testa 1994).

Differences in seal movement rates between areas were helpful in understanding overall travel patterns. As expected from the sedentary nature of young pups during the summer, Erebus Bay had the lowest movement rates of all the regions. The February and March outmigration of seals from their natal area is reflected in the higher movement rates outside of Erebus Bay during these months. The low movement rates in late April and May appear to indicate that pups were once again remaining in fairly localized areas, but because all tags stopped working by the end of May, it was impossible to determine if this was a temporary behavioral change, or represented recruitment into other colonies.

Clearly, the SLTDRs used in this study provided a significant amount of data on the diving behavior and movement patterns of Weddell seal pups that would have been impossible to collect otherwise. However, the SLTDRs did not work as well as expected: the transmission frequency was low, and both the proportion of improbable location fixes and the tag failure rate was high. While the cause of the failures during the 1992 season could not be determined, the high tag failure rates in 1993 and 1994 were due almost exclusively to antenna breakage. At this point, we have no definitive explanation for the high antenna failure rate.

Despite problems with the tags, the data collected formed the basis for the two main conclusions of this study: that the diving behavior of weaned Weddell seal pups was not strongly correlated with animal age, and that young Weddell seal pups were capable of long distance movements similar to those made by adults. Overall, post-weaning increases in dive capacity appeared to be gradual, and were probably a result of the slow increase in mass that accompanied age, rather than any dramatic change in the physiological processes related to diving. Despite the diving limitations imposed by age and size, the results of this study suggest that Weddell seal pups older than 2 months could dive deep enough to compete in the same areas and for the same prey items as adults. However, the pups may not have been able to remain at these depths for long enough to make such dives energetically efficient. Indeed, the routes selected by dispersing pups suggest that they concentrate their foraging activities in shallower areas than do the larger, more capable, adults.

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