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Seasonal diving behaviour in lactating subantarctic fur seals on Amsterdam Island

Abstract Diving behaviour was investigated in female subantarctic fur seals (*Arctocephalus tropicalis*) breeding on Amsterdam Island, Indian Ocean. Data were collected using electronic Time Depth Recorders on 19 seals during their first foraging trip after parturition in December, foraging trips later in summer, and during winter. Subantarctic fur seals at Amsterdam Island are nocturnal, shallow divers. Ninety-nine percent of recorded dives occurred at night. The diel dive pattern and changes in dive parameters throughout the night suggest that fur seals follow the nycthemeral migrations of their main prey. Seasonal changes in diving behaviour amounted to the fur seals performing progressively deeper and longer dives from their first foraging trip through winter. Dive depth and dive duration increased from the first trip after parturition (16.6 ± 0.5 m and 62.1 ± 1.6 s respectively, $n = 1000$) to summer (19.0 ± 0.4 m and 65 ± 1 s, respectively, $n = 2000$) through winter (29.0 ± 1.0 m and 91.2 ± 2.2 s, respectively, $n = 800$). In summer, subantarctic fur seals increased the proportion of time spent at the bottom during dives of between 10 and 20 m, apparently searching for prey when descending to these depths, which corresponded to the oceanic mixed layer. In winter, fur seals behaved similarly when diving between 20 and 50 m, suggesting that the most profitable depths for feeding moved down during the study period. Most of the dives did not exceed the physiological limits of individuals. Although dive frequency did not vary (10 dives/h of night), the vertical travel distance and the time spent diving increased throughout the study period, while the post-dive interval decreased, indicating that subantarctic fur seals showed a greater diving effort in winter, compared to earlier seasons.

Introduction

Subantarctic fur seals (*Arctocephalus tropicalis*) are among the most widely distributed fur seals, breeding in the south Atlantic, Indian and Pacific Oceans, mostly north of the Antarctic Polar Front on the subantarctic islands of Crozet, Macquarie, Marion, Prince Edward and north of the Subtropical Front on the temperate islands of Gough, Tristan da Cunha, Saint Paul and Amsterdam (Bester 1981; Riedman 1990; Goldsworthy 1992; Guinet et al. 1994). Subantarctic fur seal populations are increasing at most of the breeding localities after exploitation during the nineteenth century (Hes and Roux 1983; Bester 1987; Roux 1987). On Amsterdam Island, Indian Ocean, the population of subantarctic fur seals appears to have stabilized at about 50,000 individuals (Guinet et al. 1994).

Most fur seal species feed on squid and vertically migrating fish (Bester and Laycock 1985; Green et al. 1989, 1990; Klages and Bester 1998; Cherel et al. 1999), while the main prey of Antarctic fur seals breeding at South Georgia is krill (Croxall and Pilcher 1984; Reid and Arnould 1996), and the fur seals show a consistent diel diving pattern (Croxall et al. 1985; Harcourt et al. 1995). The diving pattern has been described for most otariid species where lactating females are primarily nocturnal and relatively shallow divers, with few individuals diving deeper than 200 m (northern fur seal *Callorhinus ursinus*, Gentry et al. 1986c, Goebel et al. 1991; Antarctic fur seals, *A. gazella*, Croxall et al. 1985, Kooyman et al. 1986, Boyd and Croxall 1992; Galapagos fur seals, *A. galapagoensis*, Kooyman and Trillmich 1986a, Horning and Trillmich 1997; Cape fur seals, *A. pusillus pusillus*, Kooyman and Gentry 1986; New Zealand fur seals, *A. fosteri*, Harcourt et al. 1995,

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Mattlin et al. 1998; Juan Fernandez fur seals, *A. philippi*, Francis et al. 1998; subantarctic fur seals, *A. tropicalis*, Goldsworthy et al. 1997; California sea lions, *Zalophus californianus*, Feldkamp et al. 1989, Antonelis et al. 1990; Steller sea lions, *Eumetopias jubatus*, Merrick and Loughlin 1997). All of the previous studies investigated the diving behaviour during the summer only, with the exception of Steller sea lions and New Zealand fur seals, which were also monitored in winter (Merrick and Loughlin 1997; Mattlin et al. 1998).

In subantarctic fur seals, the pup-rearing period lasts about 10 months (Bester 1981; Roux and Hes 1984; Kerley 1985) during which time lactating females alternate periods at sea to feed (foraging trips) with periods ashore to nurse their single pup (Bester and Bartlett 1990; Goldsworthy 1992; Georges and Guinet, in press a). On Amsterdam Island, foraging trip durations increase from the first trip after parturition (mean ± SD: 5.7 ± 2.6 days, $n = 85$) to summer (10.8 ± 3.1 days, $n = 85$) through winter (22.7 ± 6.6 days, $n = 24$) (Georges and Guinet, in press a, in press b). This indicates that subantarctic fur seals cope with seasonal changes in environmental conditions throughout the pup-rearing period. However, there are no published data available on the seasonal feeding ecology in subantarctic fur seals. In this study, we used electronic time depth recorders to describe diving behaviour in lactating subantarctic fur seals breeding on Amsterdam Island, from their first trip after parturition during the austral summer, to austral winter.

Materials and methods

This study was carried out at Amsterdam Island (37°55′S; 77°30′E), Indian Ocean from December 1995 to August 1996. Amsterdam Island lies 3000 km east of South Africa, 3000 km west of South Australia, and 400 km north of the Subtropical Front. There is no peri-insular shelf, and water depth increases from 0 to 500 m within a 2-km range of the island. The females used in this study were breeding at "La Mare aux Elephants", one of the island's largest breeding colonies (Guinet et al. 1994). Lactating females were caught and immobilized using a noose pole and a wooden restraining board (adapted from Gentry and Holt 1982). Mothers were then double-tagged (Dalton Rototags, Dalton Supply, Nettlebed, UK), and measured (standard body length, from nose to tail, ±1 cm; body mass, ±0.5 kg). Each female was released to her pup after an MK5 Time Depth Recorder (TDR, Wildlife Computers, Redmond, Wash.) has been deployed on her.

Nineteen females were monitored, five performing their first trip after parturition (December 1995), ten on one following trip in February/March 1996 (austral summer), and four in July 1996 (austral winter). MK5 TDRs ($64 \times 38 \times 13$ mm) were streamlined to reduce drag and had a mass of 70 g (i.e. 0.1% of seal body mass). TDRs were attached with nylon-ties to pieces of Velcro slightly larger than the base of the instrument. The Velcro sections were glued to the fur on the back between the shoulders or 10 cm from the tail of the animals with fast-set epoxy (Ciba Specialty Chemicals, Duxford, UK). Upon recapture, TDRs were removed by cutting the nylon-ties, leaving the Velcro patch attached to the seal to be shed during the annual moult.

All the TDRs were programmed to record dive depth (±1 m) and duration of dives ≥3 m every 10 s. This low sampling frequency was used to avoid memory saturation (128 Kb) during the longest foraging trips. Data were downloaded using PROCOMM version 2.43 and analysed using Wildlife Computer software (Zero Offset Correction version 1.22, Dive Analysis version 4.07). Due to the protocol and sampling rate, only dives > 4 m in depth and > 10 s in duration were used in this study. Bottom time (time spent at bottom of the dive) was taken as the time between the first and last depth readings equal to 75% of the maximum depth of the dive (Cherel et al. 1999). A visual examination of the graphs of depth over time indicated that the criterion of 75% of the dive's maximum depth to determine bottom time was appropriate for all dives investigated. Post-dive interval was defined as the lapse of time between the end of one dive and the beginning of the next dive. Average rates of descent and ascent were calculated from the beginning/end of the dive to the start/end of the bottom time. Due to the unequal number of dives recorded per seal (range: 205–2456 dives per trip), 200 dives of each individual were randomly sampled to describe the diving pattern while giving an equal statistical weight to each seal and thus reducing strong individual effects and avoiding pseudoreplication (Cherel et al. 1999). Because of the differences in night duration in the course of the year (8 h in January to 12.4 h in August), all parameters of diving effort were calculated per hour of night. Night-time was calculated according to the date of foraging trip using SUNTAB shareware (A. Lysell, Huddinge, Sweden) for the latitude of Amsterdam Island. Diving effort was investigated by considering three different parameters: Dive Frequency (number of dives/h of night), hourly Vertical Travel Distance (VTD in m/h of night, sum of the maximum depth reached per hour of night multiplied by 2; Horning and Trillmich 1997), and hourly Time Spent Diving (TSP in min/h, sum of the time spent submerged per hour of night).

Statistical analyses were carried out according to Sokal and Rolf (1981), using Systat 7.0 statistical software (Systat, SPSS). Differences between seasons in dive depth, dive duration, bottom time and post-dive intervals were tested using a nested ANOVA with individuals nested within season. Because of their skewed distributions, data were $\log_{10}$-transformed, as in Mattlin et al. (1998). Values are given as means ± SE. All tests were two-tailed and differences were considered significant at $P < 0.05$.

Results

Among the 24,880 dives recorded for the 19 monitored seals, the deepest was 208 m during a 200-s dive (seal 9632, in winter), while the longest was 390 s to a maximum of 50 m (seal 9634, in winter) (Table 1). A typical dive pattern dive is shown at different levels of detail in Fig. 1.

Daily diving activity

Ninety-nine percent of the 3800 dives sampled randomly were performed during the night. Mean dive depth was greater for night dives than for day dives (20.6 ± 0.3 m, $n = 3763$ vs 8.4 ± 0.8 m, $n = 37$; $\log_{10}$-transformed data *t*-test $t = 5.1$, $P < 0.001$) and the deepest dives occurred exclusively during the night. On average, fur seals dived to depths greater than 20 m between dusk and dawn (Fig. 2).

Over the entire sampling period, most of the dives occurred at night (97%, 99%, and 100%, respectively, for the first trips after parturition, summer, and winter, Fig. 3). The time lapse between the first and last

Table 1 Summary of data for dives >4 m in depth and >10 s in duration made by lactating subantarctic fur seals on Amsterdam Island during the first trip following parturition (*F*), later in summer (*S*) and in winter (*W*) during the 1996 reproductive season. Mean (SE) and Median (5 and 95% percentiles)

Seal ID no.	Departure	Days recorded	Season	No. of dives	Depth (m)			Duration (s)			Bottom time (s)		
					Mean	Max.	Median	Mean	Max.	Median	Mean	Max.	Median
9601	12 Dec.	10	F	372	20 (19)	95	10 (5–59)	54 (51)	250	40 (20–190)	23 (35)	180	10 (0–100)
9602	19 Dec.	6	F	772	12 (9)	58	9 (5–31)	39 (31)	200	30 (20–110)	13 (22)	130	10 (0–60)
9605	26 Dec.	6	F	442	18 (22)	135	10 (5–66)	78 (62)	290	60 (20–240)	35 (44)	220	20 (0–140)
9606	28 Dec.	5	F	696	18 (15)	97	12 (6–55)	79 (51)	320	70 (20–180)	41 (39)	200	30 (0–120)
9607	21 Dec.	7	F	205	15 (14)	95	9 (5–44)	64 (40)	190	50 (20–140)	31 (31)	110	20 (0–90)
9609	30 Jan.	10	S	1585	14 (9)	69	12 (6–34)	66 (36)	230	60 (20–130)	41 (30)	170	40 (0–90)
9611	1 Feb.	21	S	1811	18 (15)	102	13 (7–56)	54 (34)	230	50 (20–120)	30 (27)	160	20 (0–80)
9614	30 Jan.	24	S	2234	24 (20)	170	15 (6–63)	82 (43)	240	80 (20–160)	47 (38)	180	40 (0–110)
9616	4 Feb.	17	S	922	18 (16)	114	14 (5–55)	58 (36)	170	50 (20–130)	28 (33)	140	10 (0–100)
9617	2 Feb.	30	S	2175	19 (16)	104	12 (7–59)	51 (38)	200	40 (20–140)	23 (31)	130	10 (0–90)
9622	8 March	13	S	1106	17 (15)	119	13 (5–50)	51 (34)	210	40 (20–120)	23 (30)	160	10 (0–90)
9623	8 March	14	S	967	25 (23)	148	16 (5–75)	89 (51)	260	90 (20–170)	48 (44)	170	40 (0–120)
9624	9 March	13	S	621	26 (26)	153	16 (5–86)	73 (57)	260	50 (20–180)	32 (42)	170	10 (0–130)
9626	8 March	14	S	1405	16 (14)	111	13 (5–49)	70 (44)	190	60 (20–140)	38 (37)	140	20 (0–110)
9627	7 March	14	S	1862	13 (13)	116	9 (5–31)	49 (35)	200	40 (20–130)	20 (30)	150	10 (0–90)
9631	10 July	15	W	2289	24 (27)	175	12 (5–83)	69 (54)	290	50 (20–190)	27 (39)	190	10 (0–120)
9632	29 June	14	W	1655	34 (29)	208	28 (5–96)	109 (53)	260	130 (20–170)	60 (46)	230	70 (0–120)
9633	11 July	14	W	1304	25 (27)	148	12 (5–88)	64 (51)	340	40 (20–170)	25 (39)	260	10 (0–120)
9634	22 July	15	W	2456	32 (24)	202	31 (5–77)	132 (63)	390	150 (20–210)	87 (58)	210	100 (0–170)

nocturnal dive represented 92%, 90%, and 91% of night-time, during the first, summer and winter trips, respectively. There was a consistent daily diving activity over the three considered periods. During the first trip after parturition, there were significant differences in dive depth (ANOVA $F_{8,937} = 4.81$, $P < 0.001$), dive duration ($F_{8,937} = 36.61$, $P < 0.001$) and bottom time ($F_{8,937} = 25.83$, $P < 0.001$) throughout the night

Fig. 1 Example of a record of diving behaviour over a foraging trip (seal no. 9607 during its first foraging trip from 21 to 27 December 1996)
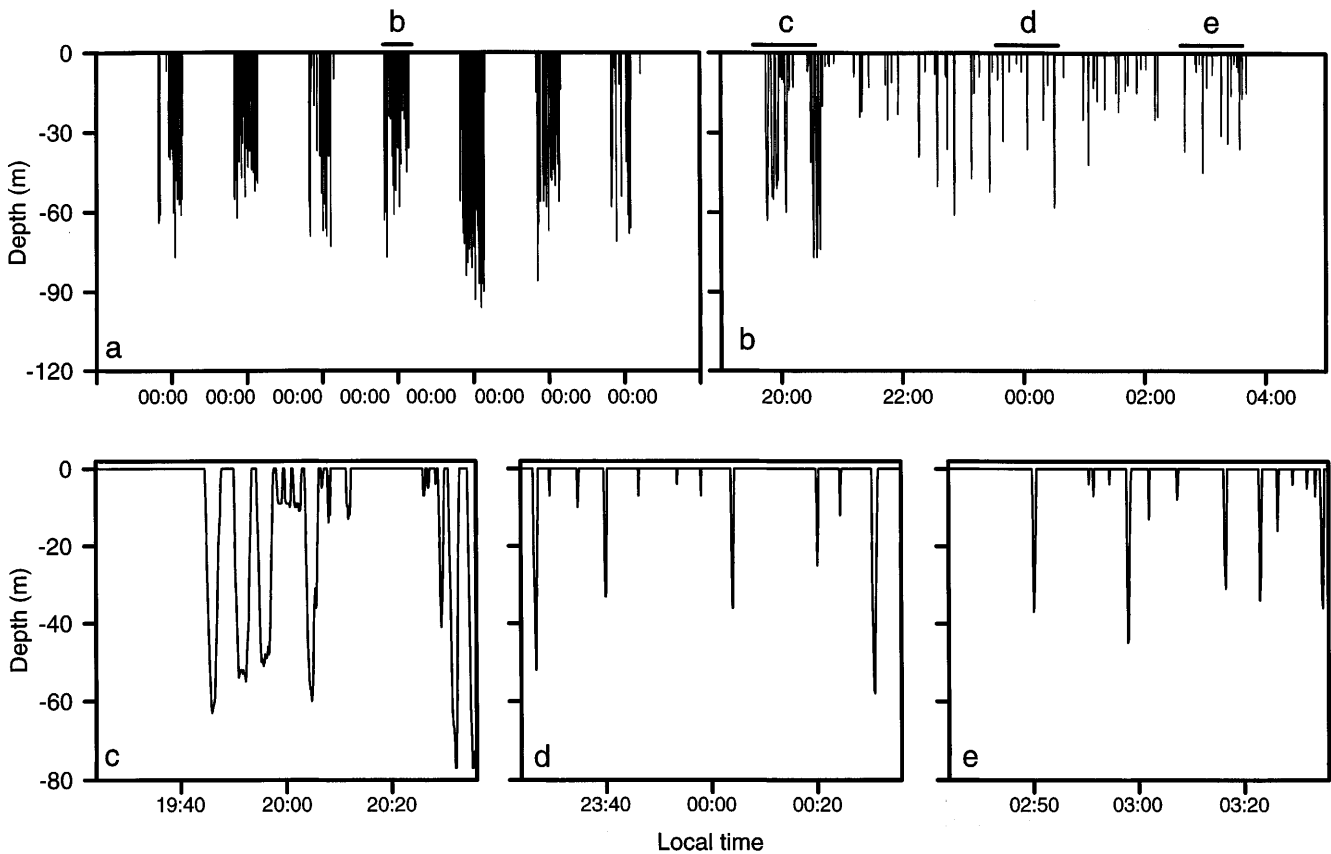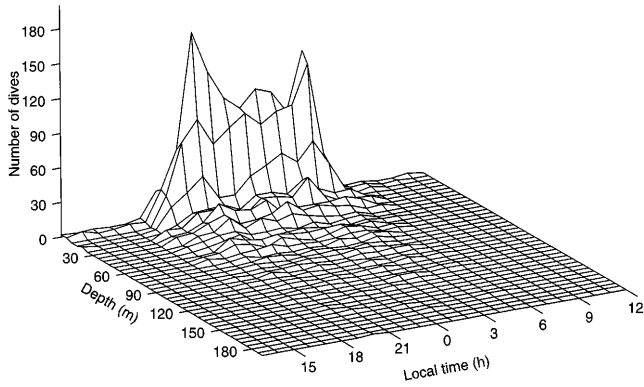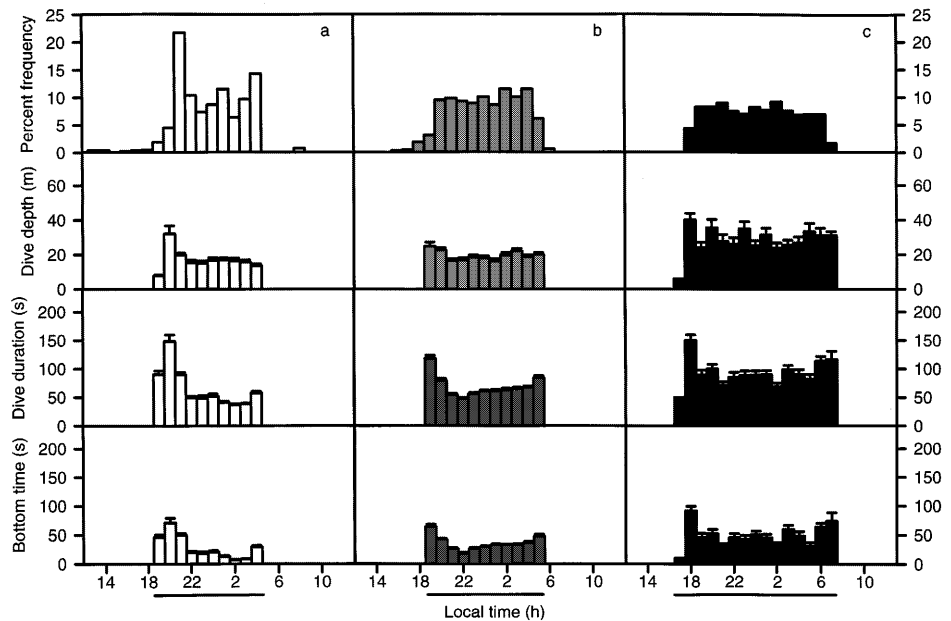
Fig. 2 Distribution of the number of dives in relation to time of the day and dive depth ($n = 3800$)

Bonferonni tests indicated that females performed longer dives with longer bottom times between 1700 and 1800 hours, and between 0500 and 0700 hours.

Seasonal diving behaviour

There were significant differences in dive depth, dive duration, and bottom time between seasons (Table 2). All of these parameters increased between the first foraging trip after parturition in December, later in summer, and winter (Tables 2, 3, Fig. 4). Differences observed in winter were due to the occurrence of two modes in diving pattern distribution. The first mode corresponded to shallow dives (5–10 m corresponding to 34% of all dives recorded in winter) similar to that found for the first trips after parturition and in summer. The second mode occurred between 10 and 45 m, which corresponded to 51% of all dives recorded in winter, and was associated with a second mode in dive duration (2–3 min) and bottom time (1.5–2 min) (Fig. 5). Furthermore, post-dive interval duration differed between seasons, being shorter in winter than during the two other seasons (Tables 2, 3). The post-dive interval duration was positively related to dive duration ($F_{1,3713} = 52.554$, $P < 0.001$), but the relationship differed between seasons because of differences in the slopes and intercepts (ANCOVA $F_{2,3713} = 3.561$, $P = 0.029$ and $F_{2,3713} = 8.532$, $P < 0.015$, respectively).

There was a general trend for dive duration to increase with dive depth, but the relationship differed between seasons (Fig. 6). During the first trip after parturition, dive duration increased with dive depth according to a linear relationship ($y = 33.0 + 1.8x$; $r^2 = 0.331$, $n = 1000$, $P < 0.001$). During later trips in summer, a power ($y = 12.253x^{0.5397}$; $r^2 = 0.306$,

(Fig. 3). Post-hoc Bonferonni tests indicated that during the first trip after parturition, dives occurring between 1900 and 2100 hours were deeper and longer with a longer bottom time, while dives between 0300 and 0400 hours were longer, had longer bottom times, but were no deeper than other dives. In summer, there were significant differences in dive depth ($F_{10,1967} = 4.74$, $P < 0.001$), dive duration ($F_{10,1967} = 17.88$, $P < 0.001$), and bottom time ($F_{10,1967} = 9.96$, $P < 0.001$) throughout the night (Fig. 3). As found for the first foraging trips, post-hoc Bonferonni tests indicated that dives between 1800 and 2000 hours were deeper and longer and with longer bottom times. Furthermore, dives between 0300 and 0500 hours were also longer and had longer bottom times than dives during the rest of the night. During winter, there were significant changes in dive duration ($F_{13,785} = 4.50$, $P < 0.001$) and bottom time ($F_{13,785} = 3.95$, $P < 0.001$) throughout the night, but not in dive depth ($F_{13,785} = 1.02$, $P = 0.09$) (Fig. 3). Post-hoc

Fig. 3 Variation in percent frequency of dives, dive depth, dive duration and bottom time with time of day during **a** the first trip following parturition, **b** later in summer, and **c** in winter during the 1996 reproductive season. Night-time is represented by a horizontal line for each season

Table 2 Mean dive performances and diving effort during the first foraging trip following parturition (1000 dives for 5 seals), in summer (2000 dives for 10 seals) and in winter (800 dives for 4 seals)

|	First trip		Summer		Winter	
	Mean	SE	Mean	SE	Mean	SE
Dive performances						
Dive depth (m)	16.6	0.5	19.0	0.4	29.0	1.0
Dive duration (s)	62.1	1.6	64.8	1.0	91.2	2.2
Bottom time (s)	28.0	1.2	33.0	0.8	48.1	1.9
Post-dive interval (min)	8.3	0.8	6.4	0.3	5.5	0.3
Rate of descent (m/s)	1.00	0.02	1.27	0.02	1.18	0.03
Rate of ascent (m/s)	1.15	0.02	1.31	0.02	1.26	0.02
Diving effort						
Dive frequency (dives/h)	9.4	1.4	8.9	0.5	10.2	0.8
Vertical travelled distance (m/h)	314	41	330	21	591	49
Time spent diving (min/h)	9.6	1.4	9.4	0.7	16.7	1.8
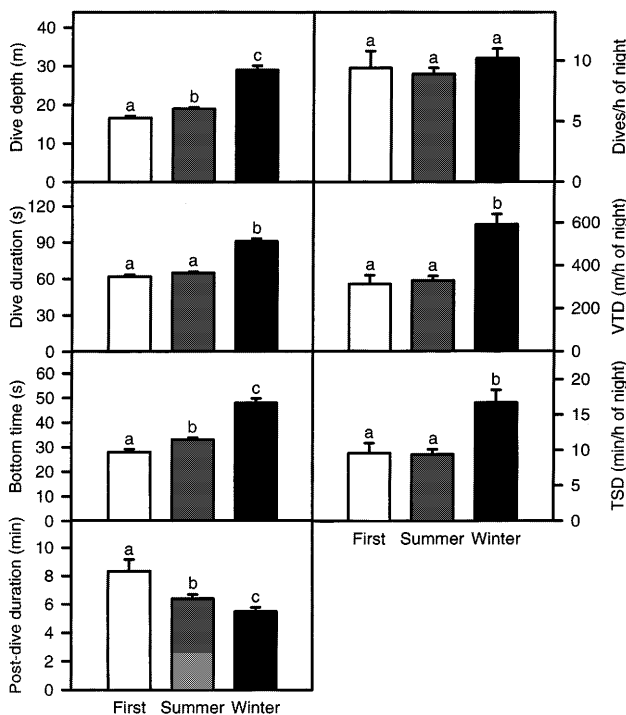
Fig. 4 Seasonal variations in dive depth, dive duration, bottom time, post-dive intervals, Dive Frequency, Vertical Travel Distance (*VTD*) and Time Spent Diving (*TSD*) during the 1996 reproductive season. Values are means ± SE. First trips after parturition *unshaded;* summer trips *grey;* winter trips *black.* Different letters indicate a significant difference between seasons (Bonferroni test, $P < 0.05$)

Fig. 5 Seasonal frequency distribution of dive depth, dive duration and bottom time during the first trip after parturition (*unshaded*), in summer (*grey*) and in winter (*black*)

$n = 2000$, $P < 0.001$) fitted better than a linear regression ($r^2 = 0.204$, $P < 0.001$) (Fig. 6). In winter, dive duration was best related to dive depth by a power ($y = 10.253x^{0.6475}$; $r^2 = 0.586$, $n = 800$, $P < 0.001$) rather than a linear relationship ($r^2 = 0.266$, $P < 0.001$). However, there was a clear bimodal distribution with dives between 20 and 50 m being as long as dives occurring between 90 and 150 m (Fig. 6). When considering dive depths by 5-m increments, dive depths between 10 and 20 m in summer, and between 20 and 50 m in winter were associated with an increase of the
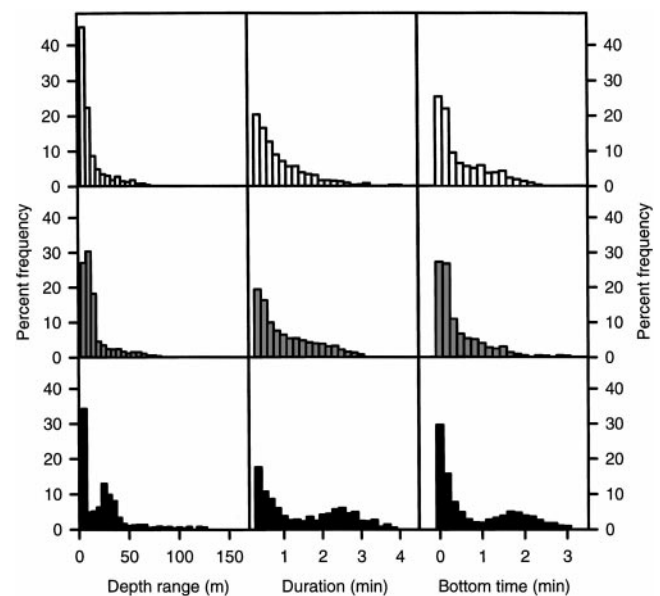
proportion of the time spent at the bottom at these depths (Fig. 6). Furthermore, the proportion of dives recorded within a 5-m class depth was positively correlated to the proportion of time spent at the bottom in the considered 5-m class depth in summer ($r_s = 0.503$, $n = 25$, $P = 0.01$), indicating that dives mostly performed by fur seals correspond to dives where they spent most of their time at the bottom. In winter, the correlation failed to significance ($r_s = 0.308$, $n = 34$, $P = 0.077$) but was significant when dives < 10 m were excluded ($r_s = 0.429$, $n = 33$, $P = 0.013$).

The mean rate of descent was significantly slower than the mean rate of ascent (paired *t*-tests for first trip: $t = 5.097$, $P < 0.001$; summer: $t = 3.828$, $P < 0.001$; winter: $t = 2.997$, $P < 0.001$; Table 2) and increased with dive depth (Fig. 6). For each season, the slope of the relationship between dive depth and descent rate was
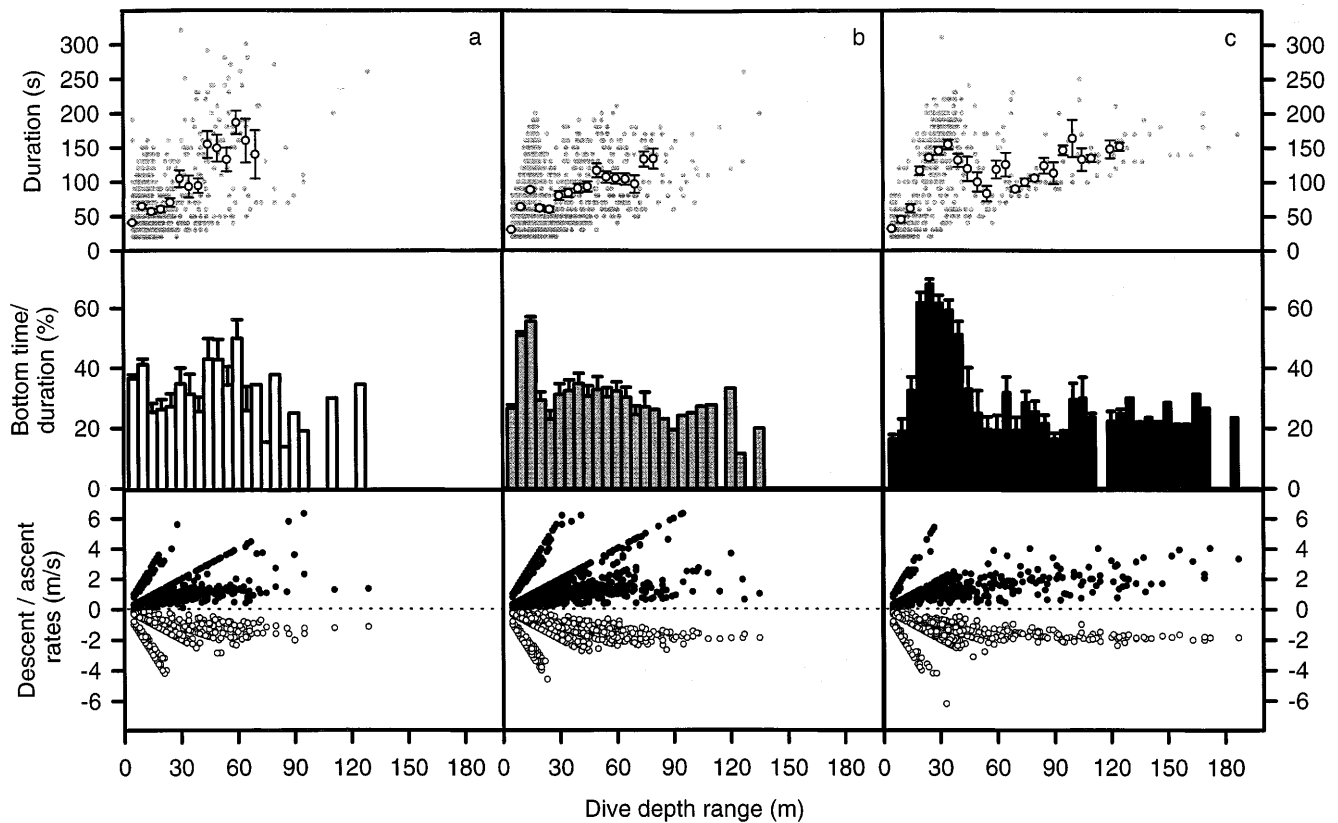
Fig. 6 Relationships between dive depth and dive duration, proportion of time spent at the bottom, and rates of descent (*filled circles*) and ascent (*unfilled circles*) during the first trip after parturition (*unshaded*), in summer (*grey*) and in winter (*black*). Values are means ± SE

significantly higher than the slope between dive depth and ascent rate (first trip: $F_{1,1996} = 19.143$, $P < 0.001$; summer: $F_{1,3996} = 22.172$, $P < 0.001$; winter: $F_{1,796} = 15.351$, $P < 0.001$). When using 5-m increments, the rates of descent and ascent only differed within a restricted dive-depth range for each season. The rate of descent was significantly slower than the rate of ascent for depths between 10 and 35 m during the first trip after parturition ($\log_{10}$-transformed data paired t-test, $P < 0.001$ in all cases), between 10 and 20 m in summer ($\log_{10}$-transformed data paired t-test, $P < 0.05$ in all cases), and between 5 and 25 m and 35 and 55 m in winter ($\log_{10}$-transformed data paired t-test, $P < 0.05$ in all cases) (Fig. 6).

Diving effort, calculated in terms of Vertical Travel Distance, and Time Spent Diving per hour of night varied throughout the study period (Table 3) but did not differ between the first foraging trip and summer (post-hoc tests, $P > 0.05$ in all cases; Table 2). Vertical Travel Distance, and Time Spent Diving per hour of night were significantly higher in winter than for the first trips after parturition and in summer (post-hoc tests, $P < 0.05$; Table 2). However, the Dive Frequency did not vary over the study period (Table 3). Although there was significant within-season variation between the individ-

ual seals' diving effort, an examination of the mean squares indicated that most of the variation in the Vertical Travel Distance and Time Spent Diving per hour of night could be attributed to between-season differences rather than within-season variation in diving effort of individual seals (Table 3).

Aerobic dive limit

The theoretical aerobic dive limit (tADL, in seconds) was estimated from the equation: $tADL = 94.2$ $(mass^{0.22})$, where mass is measured in kilograms (from Gentry et al. 1986a). The body mass of the 19 individuals studied averaged 50.0 ± 1.5 kg (range 33.0–59.0 kg), corresponding to a mean tADL of 223 s (range 203–231 s). Among the 19 seals, only 5 performed more than 1% of their dives deeper than their particular tADL (Table 4).

Discussion

Diving behaviour

Like most arctocephalines, subantarctic fur seals are nocturnal, shallow foragers (Gentry and Kooyman 1986; Goebel et al. 1991; Boyd and Croxall 1992; Harcourt et al. 1995; Francis et al. 1998; Mattlin et al. 1998), with more than 97% of dives occurring at night

Table 3 Results of nested ANOVA of dive performances (dive depth, dive duration, bottom time, post-dive interval) and hourly diving effort (dive frequency, vertical travel distance, and time spent diving per hour of night) among periods (first foraging trip after parturition, summer, and winter) in subantarctic fur seals on Amsterdam Island during the 1996 reproductive season. Data were $\log_{10}$-transformed

Source	d.f.	Mean square	F ratio	P
Dependent variable is dive depth				
Season	2	6.69	62.81	<0.001
Seal {Season}	16	1.69	15.83	<0.001
Error	3781	0.11		
Dependent variable is dive duration				
Season	2	5.34	62.91	<0.001
Seal {Season}	16	2.99	35.25	<0.001
Error	3781	0.09		
Dependent variable is bottom time				
Season	2	4.69	9.29	<0.001
Seal {Season}	16	14.40	28.49	<0.001
Error	3781	0.51		
Dependent variable is post-dive interval				
Season	2	2.36	12.63	<0.001
Seal {Season}	16	4.38	23.41	<0.001
Error	3700	0.19		
Dependent variable is dive frequency				
Season	2	0.19	1.51	0.223
Seal {Season}	16	0.42	3.31	<0.001
Error	234	0.13		
Dependent variable is vertical travel distance				
Season	2	1.64	12.09	<0.001
Seal {Season}	16	0.29	2.13	0.008
Error	234	0.14		
Dependent variable is time spent diving				
Season	2	1.49	9.24	<0.001
Seal {Season}	16	0.59	3.66	<0.001
Error	234	0.16		

Table 4 Individual dive performances and tADL in lactating subantarctic fur seals during the 1996 reproductive season

Seal ID no.	Departure	Body mass (kg)	Season	No. of dives	tADL (s)	No. of dives > tADL	% of dives > tADL
9601	12 Dec.	44.0	F	372	217	14	3.8
9602	19 Dec.	33.0	F	772	203	3	0.4
9605	26 Dec.	55.0	F	442	227	29	6.6
9606	28 Dec.	58.0	F	696	230	12	1.7
9607	21 Dec.	52.0	F	205	225	0	0.0
9609	30 Jan.	39.5	S	1585	211	9	0.6
9611	1 Feb.	46.5	S	1811	219	4	0.2
9614	30 Jan.	51.0	S	2234	224	4	0.2
9616	4 Feb.	42.0	S	922	214	0	0.0
9617	2 Feb.	51.0	S	2175	224	0	0.0
9622	8 March	47.5	S	1106	220	0	0.0
9623	8 March	57.0	S	967	229	4	0.4
9624	9 March	58.0	S	621	230	3	0.5
9626	8 March	48.0	S	1405	221	0	0.0
9627	7 March	56.0	S	1862	228	0	0.0
9631	10 July	47.0	W	2289	220	54	2.4
9632	29 June	54.0	W	1655	227	10	0.6
9633	11 July	53.5	W	1304	226	6	0.5
9634	22 July	59.0	W	2456	231	55	2.2

and rarely exceeding 100 m in depth and 4 min in duration. Throughout the year, the interval of time between the first and last nocturnal dives represented 90% of the night's duration, indicating that diving activity began after/stopped before the sun was 6° below the horizon at dusk/dawn (A. Lysell, Huddinge, Sweden). Seals changed their diving behaviour during the course of the night, as dives were longer in duration at dusk and dawn, than in the middle of the night (Fig. 3). This increase in dive duration was due to an increase in the time spent at the bottom of the dive, and was associated with an increase in dive depth at dusk (except in winter). Among subantarctic fur seals, the diel pattern of diving is consistent with the behaviour of their prey. The preferred prey of subantarctic fur seals breeding at Macquarie, Marion and Amsterdam islands are mesopelagic myctophid species that undergo diel vertical migrations, rising to the surface at night (Goldsworthy et al. 1997; Klages and Bester 1998; Y. Cherel, C. Guinet, J-Y. Georges, S. Mangin, unpublished work). The deeper dives performed by subantarctic fur seal females at dusk can be interpreted as: (1) searching dives to locate

patches of prey in the initial stages of foraging, and (2) dives during which seals feed on surface-migrating prey, as reported for Antarctic and New Zealand fur seals (Croxall et al. 1985; Boyd and Croxall 1992; Harcourt et al. 1995; Mattlin et al. 1998). The daily cycle of diving activity observed among subantarctic fur seals appears to favour the most energy-efficient means of prey capture at dusk, as has been suggested for Antarctic fur seals (Croxall et al. 1985), and New Zealand fur seals (Harcourt et al. 1995). However, the fact that subantarctic fur seals do not dive deeper at dawn while dive duration and time spent at the bottom increased during this period, suggests that they do not follow their migrating prey to lower depths but feed on prey that remained at the surface at the end of the night. Furthermore, fur seals appeared to be satiated at dawn, as has been suggested for elephant seals (Boyd and Arnbom 1991; Jonker and Bester 1994), so that they do not expend energy in diving/following their migrating prey. At Macquarie Island, subantarctic fur seals perform deeper dives at dawn (Goldsworthy et al. 1997), indicating that they follow their prey during their vertical migration, as has been observed in Antarctic and New Zealand fur seals (Croxall et al. 1985; Harcourt et al. 1995).

Dives performed by subantarctic fur seals rarely exceed tADL, suggesting that because of the diel behaviour of their prey, these seals rarely dive beyond their physiological limits, even during deep dives in winter. Similarly, lactating Antarctic fur seals generally do not dive deeper than their tADL. Such a limited diving behaviour has been related to the high metabolic rate characteristic of this species when diving (Boyd et al. 1995; Boyd and Croxall 1996). Furthermore, the positive relationship between dive duration and the duration of the subsequent post-dive interval indicates that subantarctic fur seals increase their time spent at the surface after long dives, suggesting that the costs of diving are also high in this species.

Seasonal changes

Dive duration increased with dive depth as has been widely observed among fur seals (Gentry et al. 1986a; Feldkamp et al. 1989; Harcourt et al. 1995), suggesting that fur seals maintain oxygen reserves to provide the flexibility that is necessary for long pursuits (Feldkamp et al. 1989). During the first trip after parturition, the best relationship was a linear one, but standard errors of the means of dive duration for depths deeper than 45 m suggest a reduction of the slope for high depth values. In summer, the best relationship was asymptotic (Fig. 6), as observed for Antarctic fur seals (Boyd and Croxall 1992; Boveng et al. 1996). Despite the asymptotic relationship between dive depth and dive duration in summer, subantarctic fur seals spent a relatively long time in depths between 10 and 20 m where most of the dives

were recorded. When diving to these depths, fur seals spent up to 50% of their time at the bottom of the dives (Fig. 6). Furthermore, the positive correlation between the number of dives recorded in a given class depth and the proportion of time spent at the bottom within the considered class depth in summer, suggests that subantarctic fur seals increase the number of dives at the depths where they maximize the time spent at the bottom of the dives, rather than diving to the deepest depths they can reach. This appears to be particularly important in winter as fur seals forage in a deeper column (maximum recorded dive depth 208 m) than in summer (maximum 170 m), but they perform more than 50% of their dives within a shallower water column between 20 and 50 m where they spent up to 60% of their time at the bottom of the dives. In contrast, they do not spend more than 30% of their time at the bottom during dives deeper than 60 m. This can be explained by the fact that deep dives are associated with long transit time at the expense of the time spent at the bottom. However, this also indicates that when diving between 20 and 50 m in winter, fur seals spend a longer time at the bottom of the dives than expected. Consistently, the dive duration of subantarctic fur seals is as long at depths of between 20 and 50 m as for deeper dives (> 60 m).

If the time spent at the bottom is proportional to energy gain during a dive, then this suggests that dives between 10 and 20 m in summer, and between 20 and 50 m in winter are more profitable than dives occurring at other depths. The fact that 76% of the dives were recorded between 10 and 20 m in summer suggests that most of the feeding activity occurs at the oceanic mixed layer, which is at 10–20 m (N. Metzl, personal communication), where there can be high concentrations of prey. In winter, the high proportion of dives recorded between 20 and 50 m suggests that the most profitable depths moved down and were well above the bottom of the oceanic mixed layer (520 m at 40°S in winter; Metzl et al., in press), which is beyond the diving capability of subantarctic fur seals. When diving to these apparently more profitable depths, the rate of descent was significantly slower than the rate of ascent, suggesting that these dives contain a prey-search component. When diving to deeper depths, the rates of descent and ascent did not differ, suggesting that fur seals behave similarly when swimming from/to the surface during deeper dives and they are probably without the prey-search component. In Antarctic fur seals, transit phases of deep dives are characterized by low levels of prey searching (Boyd et al. 1997). More generally, the rate of descent increased with dive depth (Fig. 6), possibly implying that subantarctic fur seals adjust the trajectory of their dives as found in Antarctic fur seals (Boyd et al. 1997). Fur seals may also anticipate the depth to which they are going to dive by increasing their swimming speed during deep dives, as observed in northern fur seals (Ponganis et al. 1992). Interestingly, the rate of ascent increased slowly with dive depth compared to the rate of descent, suggesting that

subantarctic fur seals behave similarly when ascending irrespective of dive depth.

Diving behaviour varied among individuals, but most of the variability among the parameters was related to the increase of dive depth, dive duration and time spent at the bottom during the course of the year (Fig. 4), as was found for the New Zealand fur seal (Mattlin et al. 1998). In the present study, we separated the first foraging trip after parturition from the remaining summer and winter trips because of differences in duration (Georges and Guinet, in press b) and foraging areas (J-Y. Georges, F. Bonadonna, C. Guinet, unpublished work). During their first trip after parturition, lactating females forage in the vicinity of Amsterdam Island, but travel up to 400 and 500 km during other trips in summer and winter (J-Y. Georges, F. Bonadonna, C. Guinet, unpublished work). In winter, the most visited depths are deeper than in summer, and subantarctic fur seals also increase the range of maximum depths (Fig. 5). Inter-seasonal differences in dive parameters may be due to seasonality in the oceanographic environment, such as the depth of the mixed layer (Metzl et al., in press), different foraging grounds (J-Y. Georges, F. Bonadonna, C. Guinet, unpublished work),

and probably different prey. During deep dives, fur seals may extend their searching time by diving deeper at the risk of reducing the time available for pursuit and capture of large, highly energetic prey (Dunstone and O'Connor 1979). However, diet analyses are needed to investigate diving behaviour in relation to prey types. Interestingly, the seasonal increase in dive parameters was associated with an increase in the diving effort. The number of dives performed per night spent at sea increased throughout the study period (77.2 ± 11.6, 88.1 ± 5.0 to 134.4 ± 9.9 dives per night during the first trip after parturition, and summer and winter trips, respectively). Such differences were related to the increase in the duration of the night-time from December to July, as the hourly dive frequency did not vary throughout the year (10 dives/h of night). Consequently, the Vertical Travel Distance and the Time Spent Diving per hour of night increased throughout the year because of the seasonal increase in dive depth and dive duration. Moreover, despite the increase in dive duration, the post-dive interval decreased throughout the study period, and was achieved by significant differences in the seasonal relationships between both parameters. All these results suggest that lactating subantarctic fur seals

Table 5 Comparisons of mean diving performances and diving effort (calculated per hour spent at sea) among fur seals and elephant seals. Values are means $\pm$ SE (number of individual seals), except for * (median values). *VTD* vertical travel distance, *TSD* time spent diving

Species	Dive frequency (dives/h at sea)	Dive depth (m)	Dive duration (min)	VTD (m/h at sea)	TSD (min/h at sea)
Subantarctic fur seals					
Arctocephalus tropicalis[a]	3.7 ± 0.5 (10)	19 ± 0.4	1.1 ± 1.0	140	4.1
A. tropicalis[b]	7.9 ± 0.6 (4)	12 ± 6	0.7 ± 0.3	190	5.5
Northern fur seals					
Callorhinus ursinus[c]	1.5 ± 0.2 (7)	68 ± 20	2.2 ± 0.5	204	3.3
Antarctic fur seals					
A. gazella[d,e,f]	3.4 ± 0.5 (17)	30 ± 2	0.9	204	3.1
A. gazella[g]	18.1 (385)	12.7	1.1	460	19.9
South African fur seals					
A. pusillus[h]	2.7 (2)	45	2.1	243	5.7
Galapagos fur seals					
A. galapagoensis[i,j]	5.6 ± 1.4 (3)	26 ± 4.0	1.3*	291	7.3*
Juan Fernandez fur seals					
A. phillipi[k]	0.6^1 (9)/1.9^2 (6)	$26 \pm 2/12 \pm 3$	$1.8 \pm 0.2/0.8 \pm 0.1$	31/46	1.1/1.5
Steller sea lions					
Eumetopias jubatus[l]	17.5 ± 1.2 (5)	21*	1.3	735*	22.7
California sea lions					
Zalophus californianus[m]	16.4 ± 0.8 (17)	61.8 ± 5.9	2.1 ± 0.1	1014	34.4
Galapagos sea lions					
Z. wollebaeki[n,f]	8.0 (3)	37	2.0	592	16.0
Northern elephant seals					
Mirounga angustirostris[o]	2.7 ± 0.1 (7)	400 ± 59	19.2 ± 1.6	2160	51.8
Southern elephant seals					
M. leonina[p]	2.3 ± 0.1 (8)	493 ± 20	24.4 ± 1.5	2268	56.1

[a] Present study
[b] Goldsworthy et al. (1997)
[c] Gentry et al. (1986c)
[d] Kooyman et al. (1986)
[e] Boyd and Croxall (1992)
[f] Boyd and Croxall (1996)
[g] McCafferty et al. (1998)
[h] Kooyman and Gentry (1986)
[i] Kooyman and Trillmich (1986a)

[j] Horning and Trillmich (1997)
[k] Francis et al. (1998), considering dives deeper than (1) 10 m, and (2) 3 m
[l] Merrick and Loughlin (1997)
[m] Feldkamp et al. (1989)
[n] Kooyman and Trillmich (1986b)
[o] LeBoeuf et al. (1988)
[p] Jonker and Bester (1994)

showed a greater diving effort and worked harder during the course of the year. On Amsterdam Island, subantarctic fur seals exploit distant oceanic foraging grounds (J-Y. Georges, F. Bonadonna, C. Guinet, unpublished work) during foraging trips that are long compared to those of other otariid species (Gentry and Kooyman 1986, but see Figueroa 1994; Francis et al. 1998), mothers spending about 11 and 23 days at sea in summer and winter, respectively (Georges and Guinet, in press a). Georges and Guinet (in press a) found that the rate of mass gain per day spent at sea was lower in winter than for the summer. This indicates that despite an increase in foraging effort (foraging trip duration, number of dives, dive depth, dive duration, vertical travel distance, time spent diving), maternal foraging efficiency decreased in winter, implying a lower prey availability in winter.

In summer, subantarctic fur seals performed 8.9 dives per hour of night, i.e. 3.7 dives/h spent at sea. This was similar to Antarctic fur seals (Kooyman et al. 1986), less than was found for subantarctic fur seals at Macquarie Island, Galapagos fur seals and Steller, California and Galapagos sea lions and more than for northern, South African and Juan Fernandez fur seals (Table 5). Comparisons in dive frequencies between studies should be made considering similar criteria as, for example, the minimum depth at which data are analysed (see Francis et al. 1998). Furthermore, interspecific differences in diving effort have to be carefully considered as they may be related to differences in the effective time spent diving. Among fur seal species that dive predominantly nocturnally, comparisons in dive frequency should take into account differences in the duration of the night (darkness) between localities. However, some northern fur seals dive deeply during the day (Gentry et al. 1986b; Loughlin et al. 1987), and Antarctic fur seals may perform 60% of dives during the day during years of high food availability in South Georgia (McCafferty et al. 1998), indicating that the effective time spent diving may differ among species. Furthermore, data for Antarctic fur seals indicate that interannual differences in diving effort within species may be higher than differences between species for a same locality, while data for subantarctic fur seals indicate different diving effort between localities (Table 5). This suggests that environmental conditions could to be a major factor in dive frequency and diving effort within species (see McCafferty et al. 1998). Furthermore, the present study indicates that species with a similar dive frequency may make a different diving effort when dive depth and duration are taken into account. Thus, since subantarctic fur seals have a similar dive frequency to Antarctic fur seals (Kooyman et al. 1986), their shallower dives induce a lower Vertical Travel Distance. Moreover, subantarctic fur seals have a lower Vertical Travel Distance than northern fur seals but spend more time diving. Such results may be related to differences in prey type, behaviour and availability and indicate that diving effort should consider several dive parameters, but also prey characteristics and environmental conditions, in order to assess changes between seasons and between localities for a given species and, more generally, among species.

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