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Variability in the diving activity of Antarctic fur seals, *Arctocephalus gazella*, at Iles Kerguelen

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Abstract Intra-population variation in diving behaviour of lactating Antarctic fur seals (*Arctocephalus gazella*) was studied at the Kerguelen Archipelago (49°07'S, 70°45'E) during the austral summers of 1998–2000. Dive data were successfully recorded for 112 seals equipped with time-depth recorders during 117 foraging trips. All seals displayed bouts of diving activity and the nocturnal foraging behaviour typical of otariids preying on pelagic fish and squid. Mean dive depth (53 m) was considerably deeper than recorded for this species at other sites. Four diving behaviour groups were identified: (1) deep divers ($n=60$); (2) shallow-active divers ($n=45$); (3) shallow divers ($n=9$); (4) daytime divers ($n=3$). The distribution of trips assigned to the various behavioural dive groups varied significantly between years. Antarctic fur seals at Kerguelen exhibit flexible diving strategies both within and between populations in response to changes in environmental conditions and prey availability. Electronic supplementary material to this paper can be obtained by using the Springer Link server located at <http://dx.doi.org/10.1007/s00300-001-0339-6>.

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Introduction

The diving behaviour of marine predators, quantified by the use of time-depth recorders (TDRs), is one of the most commonly used measures for differentiating foraging activity between individuals and populations, both spatially and temporally (Antonelis et al. 1990; Hindell et al. 1991; Schreer and Testa 1996; Bowen et al. 1999; Cherel et al. 1999; Bonadonna et al. 2000; Georges et al. 2000a, b). In recent years the diving behaviour of several marine predators has also been linked to spatial and temporal variability in the availability of prey species (Boyd et al. 1994; Bost et al. 1997; Swartzman and Hunt 2000; Guinet et al. 2001). Individual predators exploit prey resources in different ways. These “strategies” may vary in relation to prey availability, age and experience in terms of locating prey, and physiological limits associated with diving capabilities.

Antarctic fur seals (*Arctocephalus gazella*) are one of the most widely studied marine predators, both in terms of life history and foraging ecology. Studies of their foraging ecology have been made across their range in the Southern Ocean, from South Georgia (Boyd and Croxall 1992; McCafferty et al. 1998), Macquarie Island (Goldsworthy et al. 1997), Heard Island (Green 1997; Green et al. 1997), the Kerguelen Archipelago (Bonadonna et al. 2000; Guinet et al. 2001; Bonadonna et al., in press) to the South Shetland Islands (Costa et al. 2000; Goebel et al. 2000) and the South Orkney Islands (Daneri and Coria 1992, 1993). The breadth of data now currently recorded on the foraging behaviour of this species is one of the most comprehensive of any marine predator, revealing a flexibility in prey choice and foraging strategies between different localities and/or in relation to variability in the marine environment.

In some localities, such as South Georgia, Antarctic fur seals feed primarily on krill, with some fish species in winter and spring (North et al. 1983; Reid 1995; North 1996; Reid and Arnould 1996). Conspecifics at other

sites, such as Marion, Macquarie and Heard Islands and the Kerguelen Archipelago, feed on a more diverse range of meso-pelagic fish prey including, primarily, myctophid and nototheniid fish, and cephalopods (Cherel et al. 1997; Goldsworthy et al. 1997; Green et al. 1997). The distribution of some species of myctophid in the Southern Ocean is related to the position of the Antarctic Polar Front (APF) (Sabourenkov 1991), which varies considerably between years in the vicinity of the Kerguelen Plateau (Moore et al. 1999). Thus, variation in the diving behaviour of marine predators in response to fluctuations in prey availability in association with movement of the APF, is anticipated in the Kerguelen region.

Recent studies have identified considerable inter-population variation in diving behaviour, which is often attributed to these large-scale differences in prey type, distribution or abundance linked to differences within the marine environment (McCafferty et al. 1998; Goebel et al. 2000; Guinet et al. 2001). However, these factors may also operate at smaller spatial and temporal scales (Guinet et al. 2001), and may result in variation in diving behaviour even within a colony. As central place foragers (Orians and Pearson 1979), lactating Antarctic fur seals are limited in their exploration of the marine environment whilst foraging by the fasting capabilities of their pups. Individual differences in diving behaviour, which are thought to reflect foraging activity (Boyd et al. 1994) and, consequently, foraging efficiency (in terms of pup provisioning rates), may ultimately confer advantages in terms of breeding success.

In 1994, Boyd and co-authors stated that variation in foraging patterns between individuals within years may be attributed to differences in foraging strategies, while differences between years are attributable to changes in prey abundance. Here, we describe the classification of behavioural diving "strategies" of female Antarctic fur seals, not previously studied, at Iles Kerguelen. We aim to identify intra-population variability in diving behaviour over 3 years, and between seasons, on the basis of a range of diving parameters, using an objective clustering and multi-dimensional scaling technique.

Materials and methods

Study site

Lactating Antarctic fur seals were studied at the Kerguelen Archipelago (Fig. 1) during the austral summers of 1997/1998 (February/March), 1998/1999 (December/March) and 1999/2000 (December/March), hereafter referred to as 1998, 1999 and 2000, respectively. The seals at Cap Noir, a colony with approximately 800 breeding females situated on the northeastern coast of the Courbet Peninsula (49°07'S, 70°45'E), formed the basis of the study. Antarctic fur seals breeding on Ile de Croy, Iles Nuageuses (48°38'S, 68°38'E), located to the northwest of the archipelago, were also studied in January 2000. This colony comprises approximately 4,000 breeding females (Guinet et al. 1996; M.-A. Lea, unpublished data).

Data collection

During the 3 years, 129 time-depth recorders were deployed on females (TDRs, Wildlife Computers, Redmond, Wash.), 117 of which provided successful dive records. Three seals returned without units; one seal left the colony with her pup before the unit could be retrieved, and in seven instances the Mk7 TDR failed to record dive data. Sixteen dive records were collected with either a single Mk7 TDR ($n=7$) attached anterior to the tail or a Mk5/PTT combination ($n=6$) attached between the scapulae of female seals, at Ile de Croy, Iles Nuageuses in January 2000. Fifteen TDRs were recovered with 13 providing data. Seals were captured whilst ashore using a hoop net and were subsequently weighed, a standard length measurement recorded (nose to tail) and an individual number applied to the fur on the rump with peroxide hair-dye (Bristol-Myers Squibb, Rydalmere, Australia). During the attachment of the devices, adult seals were held on a wooden restraint board. Four TDR types were used during the 3 years (Table 1). In 1998, Mk6 Velocity TDRs or Mk5 TDR/PTT units (Bonadonna et al. 2000) were attached dorsally to the fur between the scapulae using two-part araldite (AW 2101, Ciba Specialty Chemicals). In 1999 and 2000, Mk7 TDRs replaced Mk5 TDRs, and these were attached dorsally in conjunction with a PTT, or singly, 10 cm anterior to the base of the tail.

Once TDRs were retrieved, data were downloaded directly to a portable laptop computer during the post-foraging attendance period after 1 ($n=101$), 2 ($n=14$) or 3 ($n=2$) trips to sea. Only data recorded during the first trip to sea ($n=117$) were used in this study, which included data from 5 individuals studied in consecutive years. Mk5 and Mk6 records were extracted with 3-M software, while Mk7 records were converted from hexadecimal format to decimal format with Hexdecode software (Wildlife Computers). Offset and drift of the pressure transducers were corrected using customised software (Dive-View, Bryan Dumsday). The depth resolution of TDRs was ± 1 m, except in the case of 10 Mk6 records, for which it was ± 2 m. Only dives ≥ 4 m (double the depth resolution of the least sensitive units) were included for all TDR records, thereby eliminating any travelling dives. Basic dive parameters (see below) were extracted from the decimal files using customised software (DIVE, Stewart Greenhill).

All TDRs were programmed to record depth every 5 s. Mk5 and Mk6 TDRs were returned with full memories in 13 instances. The arrival time of these seals was calculated as the midpoint between successive observational checks of the colony for maternal attendance, which were conducted at approximately 0800 and 1900 hours each day.

Bout analyses

An iterative statistical technique based on that used by Boyd et al. (1994) and modified by Harcourt et al. (in press) identified bouts of diving. Minimum criteria for inclusion as a bout were 3 dives greater than 6 m depth within a 20-min period (Boyd and Croxall 1992; Boyd et al. 1994), in order to exclude travelling dives. Once the minimum bout criteria were satisfied, the duration of the subsequent surface interval was compared to the upper 95% confidence limit of the mean surface interval within the bout. Subsequent dives were included if the surface interval was less than the mean value, which was recalculated after the inclusion of each additional dive. The bout was considered to have ended once the proceeding surface interval exceeded the recalculated confidence limit (Boyd et al. 1994; Harcourt et al., *in press*).

In order to test whether or not the observed bout pattern represented structured behaviour, rather than random distribution of dives, the dives were randomised and the bout analysis was run again. This process was repeated 1,000 times per dive record. If the number of bouts detected per replicate was greater in the random scenario than in the actual dive record in more than 95% of cases, then the dive record was considered to have bout structure (Harcourt et al., *in press*).

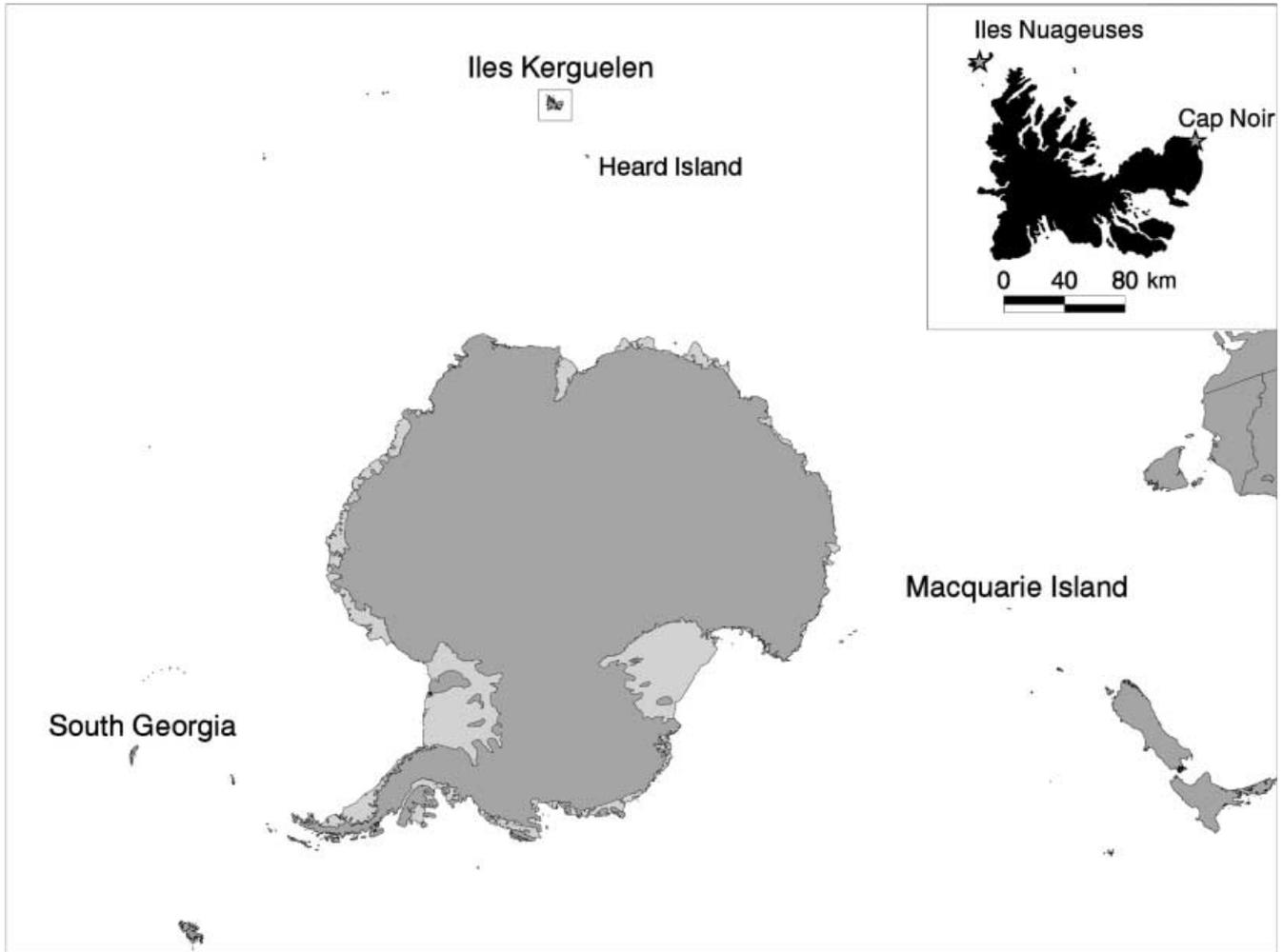


Fig. 1 Location of the study sites at Iles Kerguelen, southern Indian Ocean

Diving parameters

Twelve parameters were derived from the diving record of each seal: (1) diving frequency (number dives h^{-1}); (2) nightly diving frequency (number of dives h^{-1} of night); (3) mean depth (m); (4) mean dive duration (s); (5) proportion of time spent submerged (sum of duration of dives greater than 4 m depth, to exclude travelling behaviour), expressed as proportion of total trip duration (%); (6) proportion of night-time spent submerged (%); (7) trip duration (days); (8) proportion of dives in bouts (%); (9) number of dives per bout; (10) number of dives at night as proportion of all dives (%); (11) vertical depth travelled per hour of night (2 times the sum of nightly dive depth divided by number of night hours); (12) proportion of total vertical depth dived at night (%).

Many of the diving parameters, such as trip duration, mean depth and duration and time spent diving, have been used commonly in other studies of otariid diving behaviour (e.g. Arnould et al. 1996; Georges et al. 2000b). Preliminary exploration of the dive data also indicated that, for some seals, diving during the day constituted a considerable proportion (up to 67.2%) of the duration of the foraging trip. Consequently, we have included several variables quantifying the extent of daytime diving, i.e. proportion of dives occurring at night, proportion of total vertical depth at night and proportion of night-time spent submerged. All means are expressed as \pm standard deviation.

The duration of day and night periods was calculated based on sunrise and sunset times for Cap Noir (AUSLIG software,

Department of Industry Science and Resources, Canberra, Australia). The duration of night ranged from 7.8 to 11.5 h during the course of the study. Each dive record was also assigned a seasonal classification of either (1) early summer, for deployments from 15 December to 19 January, or (2) late summer, for deployments from 20 January to 15 March.

Statistical analysis

Quantification of differences in dive behaviour

Multidimensional scaling (MDS) is an exploratory or hypothesis-generating procedure, conducted without any assumptions of the distribution of variables (Belbin 1985). Given the lack of previous

Table 1 Summary of TDR deployments on Antarctic fur seals at Iles Kerguelen (1998–2000)

Year/season	Type of TDR			
	Mk6	PTT/Mk5	PTT/Mk7	Mk7
1998 late	10	12	0	0
1999 early	0	0	9	8
1999 late	5	0	9	3
2000 early	0	6	10	22
2000 late	1	0	12	10
Total	16	18	40	43

information concerning the diving behaviour of marine predators in the Kerguelen region, and the large sample for which diving behaviour was collected during this 3-year study, clustering and MDS techniques provided a suitably objective way of categorising the differences in diving activity of individual females both across and between years.

The seals were allocated to behavioural groups on the basis of the variables outlined above. Dive records from both study colonies were included in order to encompass as large a range of diving activity as possible for the Kerguelen region. The grand means of the 12 dive parameters for each individual dive record were included in both a cluster and an MDS analysis. A Canberra Metric association matrix was employed to construct a dissimilarity matrix (Belbin 1993), primarily on the basis of its suitability for proportional data, and as it performed highly in a comparison of 11 similarity measures (Cao et al. 1997). The Unweighted Pair Group arithMetic Averaging (UPGMA) clustering algorithm was then applied to the dissimilarity matrix (Belbin et al. 1992), and non-hierarchical agglomerative fusion strategy was then used to group similar seals and produce a dendrogram. Finally, Semi-Strong-Hybrid multi-dimensional scaling (Belbin et al. 1992) was used to enable the visualisation of the relationship between groups in three-dimensions.

A backwards discriminant function analysis (DFA) using SYSTAT 9 (SPSS) was conducted to determine the accuracy of assigning seals to a particular dive group. A jackknife analysis was then used to verify the accuracy of the DFA (Tabachnick and Fidell 1996).

Inter-annual, seasonal and inter-colony variation in dive group distribution

We tested for seasonal (early and late) and inter-annual (1998, 1999, 2000) differences in the behavioural groups for seals from Cap Noir only using the Log Likelihood Goodness of Fit test (Sokal and Rohlf 1995). The G-statistic was compared to critical values of the chi-squared distribution (Rohlf and Sokal 1995). Only dive records for individuals equipped with PTTs in late summer were included in inter-annual comparisons as no data were collected in early summer 1998 and to reduce any bias associated with deployment type. A detailed comparison of the diving behaviour and foraging ecology between *A. gazella* females breeding at Iles Nuageuses and Cap Noir will be made in a forthcoming paper.

Results

General diving behaviour

A total of 188,016 dives from 117 seals at both colonies were analysed. The maximum depth attained by any seal was 240 m during a dive lasting 5.3 min in January 2000

(Table 2). The maximum depths and dive durations for individual seals ranged from 117 to 240 m and 2.5 to 5.3 min, respectively (Electronic Supplementary Material). The mean dive depth recorded for all seals was 53 ± 17 m and mean dive duration was 1.6 ± 0.4 min. The average depths to which the seals dived on foraging trips varied considerably among individuals and ranged between 16 and 113 m. On average, $87.5 \pm 13\%$ of dives occurred at night. A diurnal pattern in diving activity and diving depth was evident for many seals, with deeper dives often occurring around dawn and dusk, and a higher proportion of seals diving between these times (Fig. 2a). The total time spent diving during a foraging trip also varied considerably among individuals (8–37%, mean = 22.5%, Fig. 2b) and was negatively correlated to foraging trip duration ($r^2 = 0.14$, $P < 0.001$, Fig. 2c), as expressed by the predictive equation:

$$\text{TSD}(\%) = 27.016 - 0.611 * \text{FTD}.$$

Bout structure was observed in the diving behaviour of 115 of the 117 seals, as shown by a greater number of bouts in the randomisations as opposed to the observed situation. Bouts occurred in the randomised situation in 76 and 87% of the cases for the other two seals (K8_00 and S2_00). After visually inspecting the two records, and given the high proportion of seals displaying bout behaviour, we decided to include the bout statistics for K8_00 and S2_00. The proportion of dives occurring in bouts ranged from 61.9 to 99.8%. The seals averaged 10.7 dives per bout (Table 2) and an absolute rate of 9.1 dives per hour, or 22.2 dives per hour of night.

Diving behaviour groups

A dendrogram of the dissimilarity in diving behaviour between the 117 foraging trips, based on the cluster analysis, indicated 4 Behavioural Dive Groups (BDG): (1) deep ($n = 60$); (2) shallow/active ($n = 45$); (3) shallow ($n = 9$) and (4) daytime ($n = 3$) divers. The daytime diving group separated out first and groups were clearly identified by MDS, with the ordination of the data in three dimensions yielding four discrete groupings with an acceptably low stress value of 0.09 (Fig. 3).

Table 2 Average diving behaviour of Antarctic fur seal females foraging at Iles Kerguelen ($n = 117$ trips)

Diving parameter	Grand mean	SD	Minimum	Maximum
Dives per hour (h^{-1})	9.1	2.8	3.9	20.8
Dives per hour of night	22.2	7.7	7.7	47.3
Mean depth (m)	53	17	16	113
Mean duration (min)	1.6	0.4	0.5	2.6
Time spent diving (%)	22.5	5.0	8.1	37.2
TSD at night (%)	50.1	10.3	19.3	70.0
Trip length (days)	7.4	3.1	2.7	17.9
Proportion of dives in bouts (%)	94.4	5.4	61.9	99.8
Number of dives per bout	10.7	1.7	8.2	16.6
Number of dives at night (%)	87.5	13.1	32.8	99.8
Depth per hour of night (m h^{-1})	1956	473	838	3020
Vertical depth at night (%)	80.7	18.3	19.6	99.9

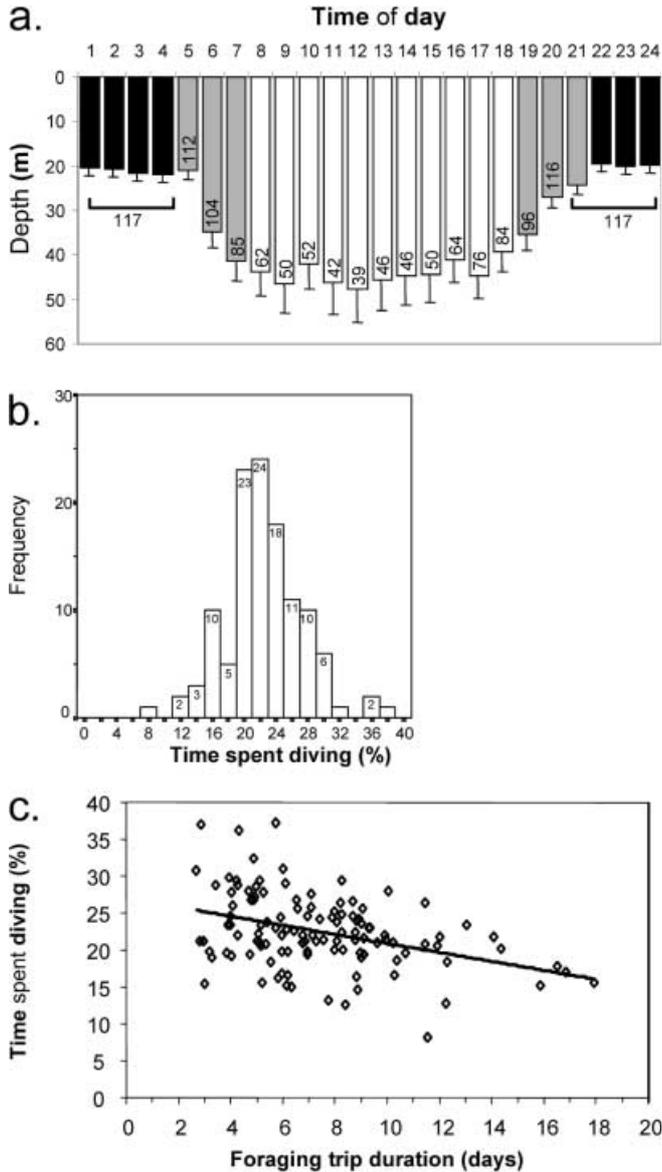


Fig. 2 **a** Maximum dive depth of Antarctic fur seals at Iles Kerguelen in relation to time of day (error bars denote 1 standard error; sample sizes are noted in or below bars). **b** Frequency histogram of time spent diving during a foraging trip ($n=117$). **c** The relationship between time spent diving and foraging trip duration

The difference in dive behaviour between the four groups in relation to time of day is displayed in Fig. 4. The “deep” diving seals sustained greater depths on average (63 m) than other seals and spent 24% of their time at sea diving (Table 3). Seals in the “shallow-active” BDG2 spent a similar proportion of their time at sea diving (22.2%). Seals in this group dived more shallowly on average to 41 m depth and dived at the highest rate (11.1 dives per hour). The “shallow” diving seals of BDG3 can be distinguished from the shallow-active seals in BDG2 by the lower amount of time spent diving (14.5%), although seals were diving to similar mean depths (36 m). Seals in this group also recorded the lowest proportion of

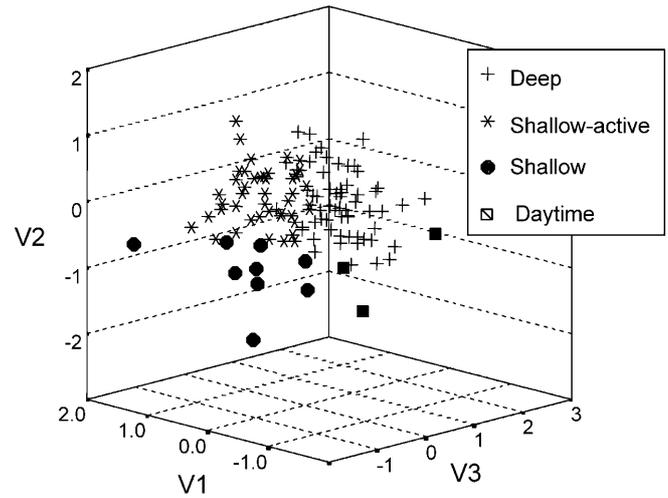


Fig. 3 Behavioural dive groups of female Antarctic fur seals as produced by multidimensional scaling and plotted in three dimensions

dives in bouts (82%) and the lowest number of dives per bout (9.5). Only three seals displayed the daytime diving typical of BDG4 (see Electronic Supplementary Material). Time spent diving at night was particularly low for these seals, with only 59% of dives occurring at night.

The morphological characteristics of the female seals in terms of length (cm) and mass (kg) did not vary as a function of behavioural dive group when tested by ANOVA (length $F_{3,116}=0.516$, $P=0.671$; mass $F_{3,116}=1.064$, $P=0.367$). Examples of diving records for seals from each of the diving categories are shown in Fig. 5.

A backwards DFA was conducted for seals in BDG1, 2 and 3. Seals in BDG4 accounted only for 2.5% of the population and were excluded due to low sample size (1.7% from Cap Noir and 0.8% Iles Nuageuses, see Electronic Supplementary Material). The DFA correctly assigned 94% of seals to behavioural diving groups using 10 of the 12 diving parameters (daytime divers excluded). Cross-validation using a jackknife analysis found 96% of the seals to be correctly assigned. The two diving parameters removed from the analysis were those largely responsible for the distinction between daytime diving seals (proportion of time spent diving at night and the percentage of dives occurring at night).

The canonical scores clearly distinguishing the three dive groups are plotted in Fig. 6. The first discriminant function accounted for 72.4% of the between-group variability, while 27.6% was accounted for by the second.

Seasonal, inter-annual and inter-colony variation in behavioural dive groups

Season

No difference in the diving behaviour of seals between early and late summer was apparent in either 1999 (Fig. 7a) or in 2000 (Fig. 7b).

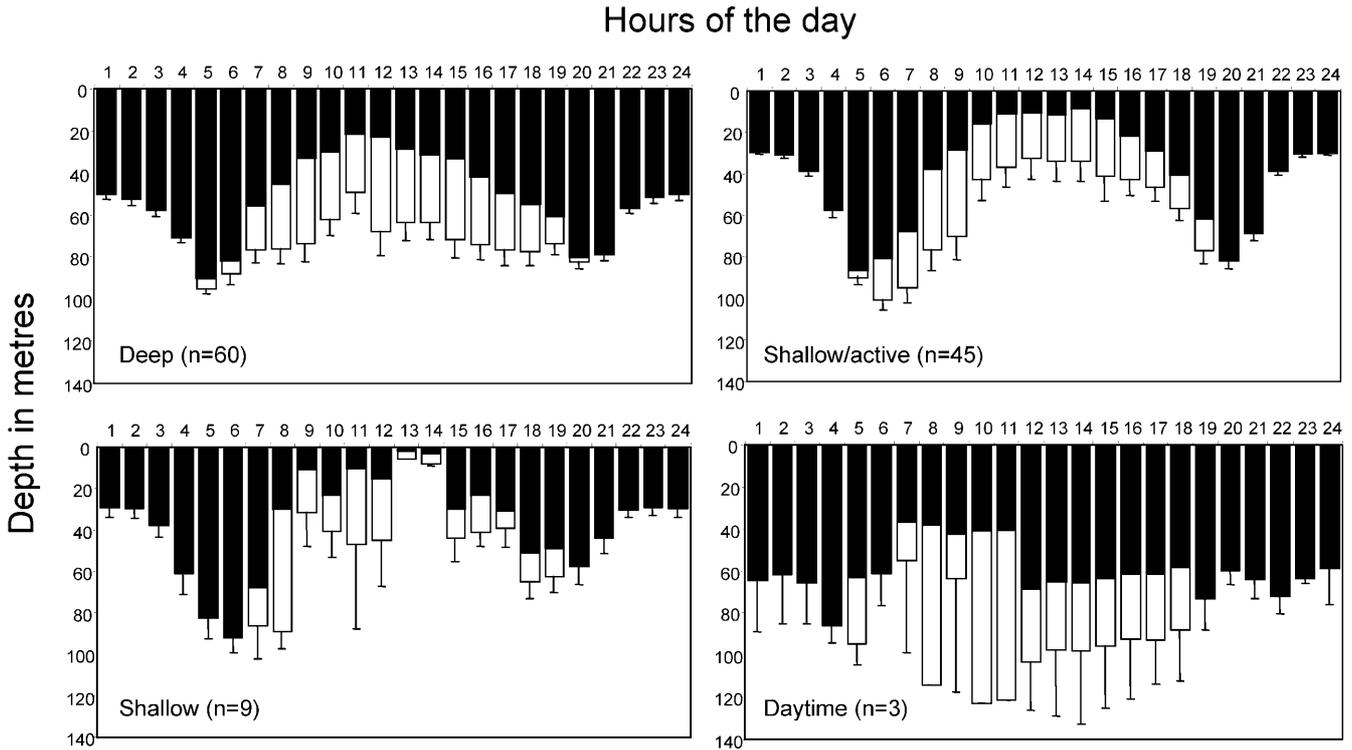


Fig. 4 Mean dive depth of seals in the four behavioural dive groups in relation to time of day. *Black bars* depict the proportion of seals per group diving in a particular hour (a *full black bar* indicates 100% of seals dived in that hour). Error bars are +1 SE

Colony

No significant difference between the types of diving behaviour of seals at Iles Nuageuses ($n=12$) and at Cap Noir ($n=25$) was evident in early lactation 2000 ($G=4.12 < \chi^2_{2,0.05}$). However, there appeared to be a higher proportion of shallow/active diving seals at Cap Noir (Fig. 7c).

Year

A comparison of the proportion of seals fitted with PTTs assigned to BDGs in late summer indicated a highly significant difference in the frequency distribution of dive groups between years ($G=10.05 > \chi^2_{4,0.05}$). This appears to be due to a shift from the high proportion of deep diving seals in 1998 to a more even distribution between these two diving behaviours in 2000 (Fig. 7d).

Of the five seals studied in consecutive years, four seals were assigned to the same BDG in both years (BDG1 $n=3$, BDG2 $n=1$) and one seal was assigned to BDG3 in 1998 and BDG1 in 1999.

Table 3 Summary statistics of diving parameters for four behavioural dive categories as identified by clustering (*mean value of maternal mass at deployment and retrieval of the TDR, N no. of trips)

Diving parameters	Behavioural dive group			
	1 Deep	2 Shallow/active	3 Shallow	4 Daytime
N	60	45	9	3
Length (cm)	116.8 ± 5	115.3 ± 5	117.1 ± 4.1	117.7 ± 5.1
Maternal mass (kg)*	32.4 ± 4.0	31.5 ± 4.6	31.1 ± 3.5	31.9 ± 1.4
Dives per hour (h^{-1})	7.8 ± 1.6	11.1 ± 2.4	9.2 ± 4.6	6.2 ± 2.0
Dives per hour of night	17.9 ± 3.5	29.1 ± 5.7	21.9 ± 10.3	8.1 ± 0.7
Mean depth (m)	63 ± 15	41 ± 7	36 ± 11	76 ± 15
Mean duration (min)	1.9 ± 0.3	1.2 ± 0.2	1.1 ± 0.3	2.0 ± 0.2
Time spent diving (%)	24.1 ± 4.9	22.2 ± 3.6	14.5 ± 2.9	20.1 ± 7.1
TSD at night (%)	51.1 ± 8.7	53.9 ± 7.0	32.6 ± 6.6	25.9 ± 2.9
Trip length (days)	6.2 ± 2.4	7.7 ± 2.6	13.1 ± 3.8	8.8 ± 2.5
Proportion of dives in bouts (%)	95.9 ± 2.2	94.9 ± 4.3	82.3 ± 9.4	91.9 ± 5.1
Number of dives per bout	11.0 ± 1.7	10.6 ± 1.6	9.5 ± 0.9	9.9 ± 1.1
Number of dives at night (%)	84.0 ± 13.9	92.9 ± 5.5	92.4 ± 6.6	59.0 ± 33.4
Depth per hour of night ($m h^{-1}$)	1977 ± 492	2105 ± 314	1362 ± 317	1088 ± 203
Vertical depth at night (%)	77.4 ± 20.7	85.4 ± 11.9	87.1 ± 9.6	57.1 ± 38.6

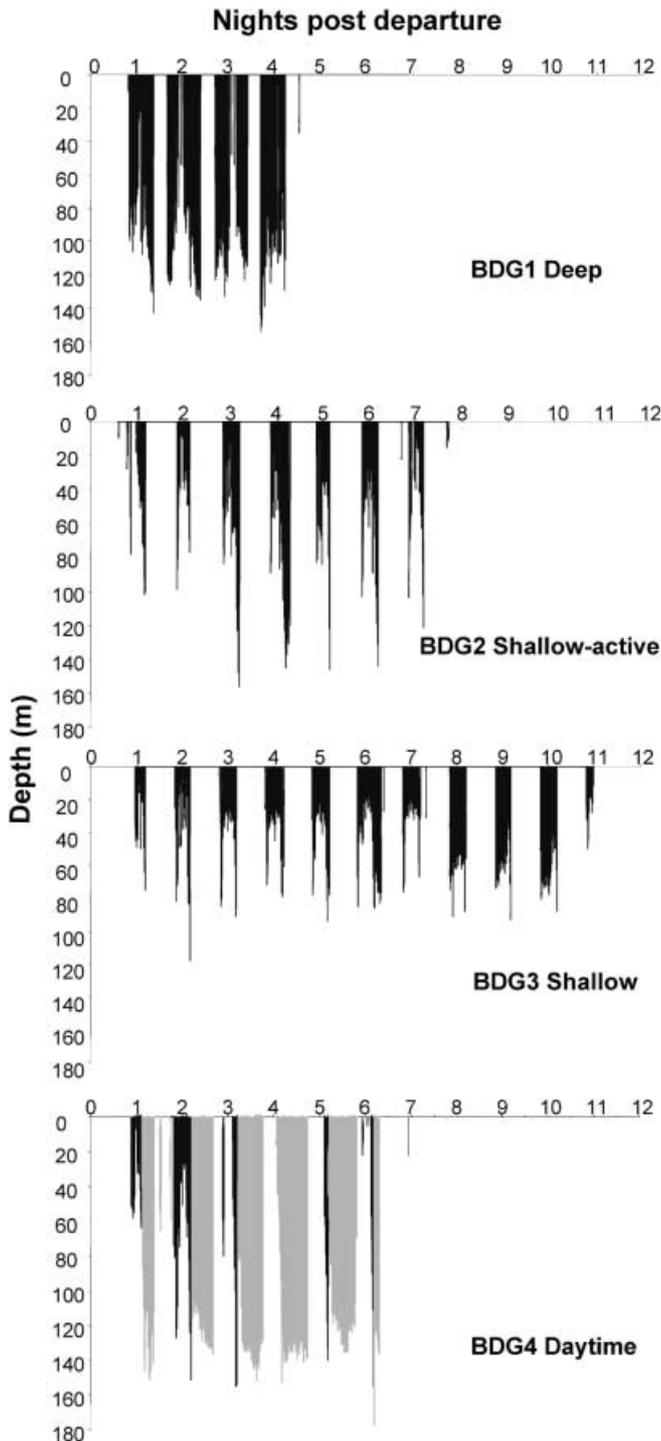


Fig. 5 Diving records plotted in two dimensions of four female Antarctic fur seals assigned to the deep behavioural dive group (BDG) 1, the shallow-active BDG2, the shallow BDG3 and the daytime BDG4 (daytime dives in grey)

Discussion

The range in diving activity recorded for lactating Antarctic fur seals at Iles Kerguelen in this study confirms previous observations of the flexibility of foraging strategies for this species (McCafferty et al.

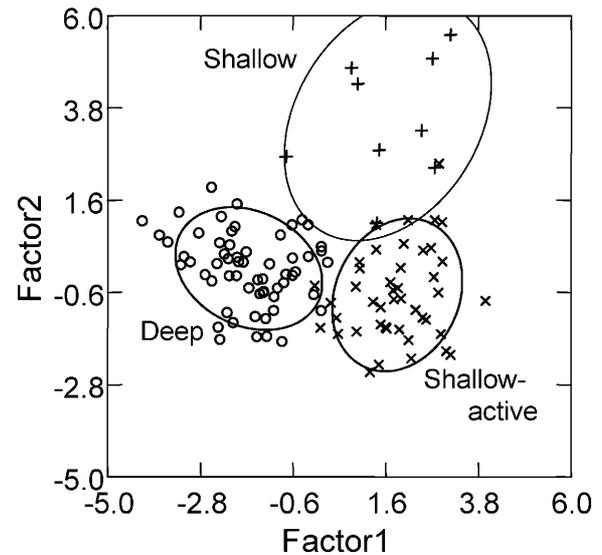


Fig. 6 The canonical scores plot for seals in the deep ($n=60$), shallow-active ($n=45$) and shallow ($n=9$) behavioural dive groups

1998; Boyd 1999). Most seals displayed shallow, nocturnal diving activity with deeper crepuscular dives, characteristic of fur seals preying on pelagic species (Boyd and Croxall 1992; Goldsworthy et al. 1997). However, considerable intra-population variation was evident on the basis of several diving parameters, particularly the proportion of vertical depth attained at night, the proportion of time spent diving overall and at night, and the number of dives per hour or per hour of night. For example, three seals (two in 1998 and one in 2000) conducted a high proportion of dives during daytime, while most seals only dived at night.

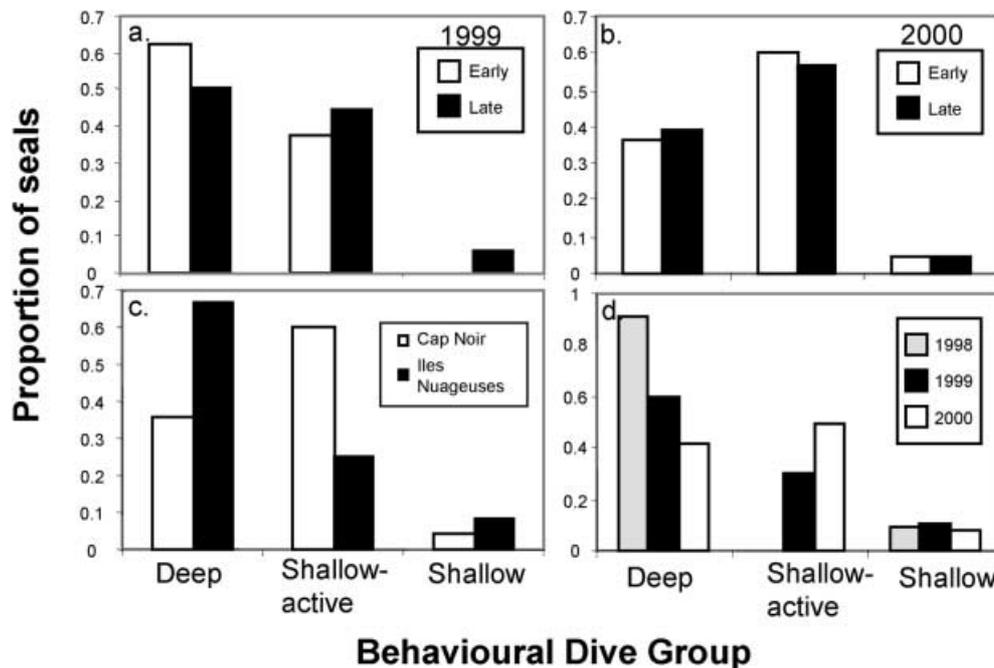
Diving behaviour categories

Although much inter-individual variation in dive behaviour was apparent, our analyses revealed four broad diving categories or strategies. Some individual variation within the groups may be due to factors such as TDR type; however, it is difficult to account for such effects given the multi-year, multi-season and multi-site nature of the data.

Behavioural Dive Group 1 – deep divers

The majority of dive records (51.2%) were assigned to the deep-diving behavioural group. These seals dived to both deeper absolute (240 m) and mean depths (39–113 m, mean = 63 m) at the Kerguelen Archipelago than at any other site where the diving behaviour of female Antarctic fur seals has previously been studied (Table 4). Female seals at Heard Island (Green 1997), also positioned on the Kerguelen Plateau, are the only population of Antarctic fur seals reported to display mean

Fig. 7a–d The frequency distribution of Antarctic fur seals assigned to three diving activity categories. **a** 1999 seasonal comparison. **b** 2000 seasonal comparison. **c** Inter-site comparison between Cap Noir and Iles Nuageuses in early summer 2000. **d** Inter-annual comparison (1998–2000)



diving depths (10–47 m) approaching those of the seals in this study. It is possible the low mean dive depth (13 m) of Antarctic seals studied at Bird Island (McCafferty et al. 1998) could be explained by the lower minimum dive depth criterion of ≥ 1 m (Table 4). Approximately 68% of dives over the 3 years of the study were ≤ 4 m. If an equivalent proportion of 1-m dives are incorporated into the mean diving behaviour of the 117 seals in this study (Table 2), a dive depth of 18 m is obtained. However, while dive depths of 1–2 m may represent foraging by seals on surface-swarming krill at South Georgia, shallow dives at Kerguelen would likely represent either pressure transducer variability, given the resolution of some TDRs, and/or surface travelling dives. In addition, nocturnal trawls conducted for myctophids in the vicinity of Kerguelen by Duhamel et al. (2000) indicated high abundances of species preyed upon by Antarctic fur seals occurring well below the surface at 50 m.

On average, seals in BDG1 also conducted shorter foraging trips than other seals, and while the majority of dives were conducted at night, more daytime dives were recorded than for the more shallow-diving seals. Given the large proportion of dives in bouts (96%), the relatively short duration of foraging trips and the consistent nocturnal diving rate (18 dives h^{-1} of night) of deep-diving seals at Kerguelen, it is probable that seals were travelling to a relatively constant or reliable pelagic food source, which could only be accessed at considerable depth. Antarctic fur seals foraging over the continental shelf near Cape Shirreff, Antarctica, were found to dive deeper with a higher proportion of daytime dives than those diving on the shelf break or over deep water (Goebel et al. 2000). The diving patterns of northern fur seals, *Callorhinus ursinus*, studied at St. Paul Island, also

separated primarily on the basis of depth. Deep divers expended less energy diving than shallow divers, while apparently obtaining greater energy per dive (Goebel et al. 1991). Deep-diving northern fur seals fed principally on benthic fish species over the continental shelf (Goebel et al. 1991), whilst the majority of seals tracked at Cap Noir concentrated their foraging activity in waters greater than 500 m on the edge of the Kerguelen Plateau (Guinet et al. 2001). Future research will focus on the relationship between diving strategies, location at sea and the foraging success in terms of pup provisioning of individual seals.

Behavioural Dive Group 2 – shallow-active divers

Seals diving shallowly and more actively ($n=40$) conducted the majority of their dives at night. Mean dive depths, while still deeper than for most populations of Antarctic fur seals, were shallow for seals breeding at Kerguelen, ranging from 25 to 54 m. This pattern of diving, with relatively elevated rates of time spent diving and vertical depth travelled per hour of night, is consistent with dive behaviour noted for other populations of Antarctic fur seals at, for example, Macquarie Island where seals also feed primarily of myctophid fish, and at South Georgia where seals feed primarily on shallow schooling krill (Reid and Arnould 1996).

Behavioural Dive Group 3 – shallow divers

The overall and nightly proportion of time spent diving by seals in BDG3, 14.5 and 32.6% respectively, was low in comparison to the other shallow-diving seals of BDG2

Table 4 Inter-population comparison of diving activity for Antarctic and northern fur seals at various sites [*t* number of trips; * median value; # time spent diving calculated for trip duration excluding transit times; *F* fish; *S* squid; *K* krill. Time spent diving (*TSD*) is interpreted as the amount of time spent submerged]

Species		<i>n</i>	Mean depth (m)	Trip length (days)	TSD (%)	Diet	Depth criterion	
Antarctic fur seal	Kerguelen ^a	Deep	60 ^f	63	6.2	24.1	F+S ^j	≥4 m
		Shallow/active	45 ^f	41	7.7	22.2	F+S	≥4 m
		Shallow	9 ^f	36	13.1	14.5	F+S	≥4 m
		Daytime	3 ^f	76	8.8	20.1	F+S	≥4 m
		Mean	117 ^f	53	7.4	22.5	F+S	≥4 m
		South Georgia	1988/1989–1989/1990 ^b	11	8–19*	2.5–8	13.6	K
Heard Island ^d	1992	3	13.2	–	–	F+S	≥5 m	
	1993	9	36.1	–	–	F+S	≥5 m	
Macquarie Island ^c	1991	14	12±11	2.5	10.4	F+S	>2 m	
Cape Shirreff	1998 ^f	11	13.3–20.6	4.6	–	K+F	≥4 m	
	1998 ^g	14	19	4.54	9.8	K, F, F+K	≥4 m	
Northern fur seal	St Paul Island ^h	Deep	4	84.5	–	–	F+S	–
		Shallow	5	43.7	–	–	F+S	–
	St George Island	1980,1982	7	68	7.5	–	F+S	–

^aThis study

^bBoyd and Croxall (1992)

^cMcCafferty et al. (1998)

^dGreen (1997)

^eGoldsworthy et al. (1997)

^fGoebel et al. (2000)

^gCosta et al. (2000)

^hGoebel et al. (1991)

ⁱCherel et al. (1997)

(23.2 and 53.9% respectively). In addition to the reduced proportion of dives in bouts and number of dives per bout for this group, it appears that seals may be spending a higher proportion of their time at sea searching for prey and/or feeding on a less aggregated prey source than more active, shallow-diving seals of BDG2.

Arnould et al. (1996) found a close negative sigmoidal relationship between at-sea metabolic rate and the proportion of time at sea spent diving, in a study of the at-sea metabolism of female Antarctic fur seals at Bird Island, South Georgia. The authors suggested the measure (time spent diving) could provide a useful and inexpensive estimate of energy expenditure. At-sea metabolism was not measured at Iles Kerguelen; however, the reduced proportion of time at sea spent diving for this group may reflect a higher metabolic rate for these seals. Costa et al. (2000), in a study of the foraging energetics of Antarctic fur seals at Livingston Island, found no such relationship and suggested that the high field metabolic rates (FMR) recorded were due to a large proportion of surface swimming as only 10% of time at sea was spent diving.

Based on the findings of Arnould et al. (1996) and Costa et al. (2000), we hypothesise that seals in BDG2 had higher FMRs than other seals, due in part to higher levels of surface swimming while searching for prey patches (see Bonadonna et al. 2000).

Behavioural Dive Group 4 – daytime divers

This small group, representing 2.5% of foraging trips studied, included a high proportion of daytime dives to

average depths far greater than those for other groups. We may have expected these seals to be larger in terms of length and mass, as a direct relationship exists between the diving capability of a marine mammal and its metabolic stores (Kooyman 1989 in Costa et al. 2000). However, no difference in size was found between seals in the different behavioural dive groups. This may be due in part to the low numbers of seals ($n=3$) exhibiting this particular behaviour.

Few studies have examined longitudinal trends in the foraging strategies of fur seals. McCafferty et al. (1998) observed female identity to be important in explaining variation in foraging trip duration and in diving activity of Antarctic fur seals at Bird Island, while at Iles Kerguelen, Bonadonna et al. (in press) found the direction taken by seals fitted with satellite transmitters during consecutive foraging trips to be similar. Of the small number of seals studied in consecutive years in this study, 80% were assigned to the same behavioural dive group in both years, highlighting the importance of longitudinal studies in examining foraging strategies.

Inter-population comparisons of dive behaviour

It is apparent that the diving activity of seals in the Kerguelen region differs from that of conspecifics at other sites (see Table 4). Unfortunately, quantitative comparisons of diving behaviour between sites are hindered by differences in both methodology (TDR types and sampling protocols) and analysis techniques. For example, the lower minimum depth criterion of many studies will reduce the average dive depth recorded for

these seals. However, some general patterns are apparent, particularly that seals at Iles Kerguelen dive more deeply while making longer foraging trips than do seals from other populations, such as at Macquarie (Goldsworthy et al. 1997) and Heard Islands (Green 1997), where seals feed on similar prey. In many respects the diving activity of *A. gazella* females at Kerguelen differs from the diving behaviour of krill-feeding Antarctic fur seal populations, and in fact appears more similar to that of northern fur seals, the Arctic counterpart of Antarctic fur seals (Table 4). The higher incidence of consistently deep diving behaviour at Iles Kerguelen than at other breeding sites, particularly in 1998, raises questions about the prey availability and variability of the marine environment around the archipelago. Examination of the relationship between behavioural dive groups and the spatial utilisation of the marine environment by seals should further clarify the ecological significance of the dive groupings.

Georges et al. (2000b), studying sub-Antarctic fur seals (*A. tropicalis*) at Amsterdam Island, observed that seals exhibited markedly different diving behaviour between the first trip after parturition, in summer, and in winter. Seals increased their time spent diving in winter, diving to greater depths, indicating that a greater diving effort was required at this time. Maternal foraging efficiency in winter decreased in comparison to earlier months (Georges and Guinet 2000) implying lower prey availability in winter (Georges et al. 2000a).

Seasonal differences in diving behaviour were not observed at Iles Kerguelen. The lactational period of Antarctic fur seals (4 months) is relatively short in comparison to that of sub-Antarctic fur seals (10 months), which forage further from their colonies in winter months (up to 530 km) when the Sub-Tropical Front migrates further north of Amsterdam Island (Georges et al. 2000a). However, inter-annual and inter-colony differences in the distribution of seals within the different behavioural groups were observed at Iles Kerguelen. This finding implies that our method of diving-activity classification may be sufficient to identify temporal and spatial variation in diving activity linked to changes in the marine environment and the distribution of prey. The highly predictive nature of the discriminant function analysis also implies that this method, at least at Kerguelen, is not only sufficient but also relatively accurate at differentiating between the diving strategies of seals. The difference observed in proportion of deep versus shallow divers between seals at Cap Noir and Iles Nuageuses in January 2000 indicates that small-scale, localised changes in marine conditions and, potentially, prey availability affect the diving behaviour of seals.

Conclusions

This study has highlighted the degree of flexibility possible in the diving behaviour of Antarctic fur seals on

both an intra- and inter-population level. The differences observed in diving activity between the four groups may reflect differences in prey availability, both in terms of depth and patchiness, as well as the foraging experience and metabolic limits of the individual seals. Whilst the four types of behavioural dive groups have been reported to some extent at other sites, the occurrence of all four together has not previously been noted. The variability in the number of seals using each behavioural dive group between sites and years indicates a shift in dive pattern in response to environmental conditions.

Finally, Bonadonna et al. (in press) recently demonstrated that some Antarctic fur seals return to similar foraging zones in successive foraging trips, suggesting some degree of site fidelity in relation to past experience. A longitudinal examination of the dive behaviour of individuals is necessary to fully interpret the importance of learnt foraging areas to the diving strategies of individual seals.

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References

- Antonelis GA, Stewart BS, Perryman WF (1990) Foraging characteristics of female northern fur seals (*Callorhinus ursinus*) and California sea lions (*Zalophus californianus*). *Can J Zool* 68:150–158
- Arnould JPY, Boyd IL, Speakman JR (1996) The relationship between foraging behaviour and energy expenditure in Antarctic fur seals. *J Zool Lond* 239:769–782
- Belbin L (1985) A background briefing in numerical taxonomy, or does your handbag match your shoes. DECUS Symposium, Hobart, Australia
- Belbin L (1993) PATN pattern analysis package – technical reference. Division of Wildlife and Ecology, CSIRO Australia
- Belbin L, Faith DP, Milligan GW (1992) A comparison of two approaches to beta-flexible clustering. *Multivar Behav Res* 27:417–433
- Bonadonna F, Lea M-A, Guinet C (2000) Foraging routes of Antarctic fur seals (*Arctocephalus gazella*) investigated by the concurrent use of satellite tracking and time-depth recorders. *Polar Biol* 23:149–159
- Bonadonna F, Lea M-A, Dehorter O, Guinet C (in press) Foraging ground fidelity and route-choice tactics of a marine predator: the Antarctic fur seal (*Arctocephalus gazella*). *Mar Ecol Prog Ser*
- Bost CA, Georges J-Y, Guinet C, Cherel Y, Putz K, Charrassin J-B, Handrich Y, Zorn T, Lage J, Le Maho Y (1997) Foraging habitat and food intake of satellite tracked king penguins during the austral summer at Crozet Archipelago. *Mar Ecol Prog Ser* 150:21–33

- Bowen WD, Boness DJ, Iverson SJ (1999) Diving behaviour of lactating harbour seals and their pups during maternal foraging trips. *Can J Zool* 77:978–988
- Boyd IL (1999) Foraging and provisioning in Antarctic fur seals: interannual variability in time-energy budgets. *Behav Ecol* 10:198–208
- Boyd IL, Croxall JP (1992) Diving behaviour of lactating Antarctic fur seals. *Can J Zool* 70:919–928
- Boyd IL, Arnould JPY, Barton T, Croxall JP (1994) Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. *J Anim Ecol* 63:703–713
- Cao Y, Williams P, Bark AW (1997) Effects of sample size (replicate number) on similarity measures in river benthic Aufwuchs community analysis. *Water Environ Res* 69:107–114
- Cherel Y, Guinet C, Tremblay Y (1997) Fish prey of Antarctic fur seals *Arctocephalus gazella* at Ile de Croix, Kerguelen. *Polar Biol* 17:87–90
- Cherel Y, Tremblay Y, Guinard E, Georges J-Y (1999) Diving behaviour of female northern rockhopper penguins, *Eudyptes chrysocome moseleyi*, during the brooding period at Amsterdam Island (Southern Indian Ocean). *Mar Biol* 134:375–385
- Costa DP, Goebel ME, Sterling JT (2000) Foraging energetics and diving behaviour of the Antarctic fur seal *Arctocephalus gazella*, at Cape Shirreff, Livingston Island. In: Davidson W, Howard-Williams C, Broady P (eds) Antarctic ecosystems: models for wider ecological understanding. New Zealand Natural Sciences, Christchurch, pp 77–84
- Daneri GA, Coria NR (1992) The diet of Antarctic fur seals, *Arctocephalus gazella*, during the summer-autumn period at Mossman Peninsula, Laurie Island (South Orkneys). *Polar Biol* 11:565–566
- Daneri GA, Coria NR (1993) Fish prey of Antarctic fur seals, *Arctocephalus gazella*, during the summer-autumn period at Laurie Island, South Orkney Islands. *Polar Biol* 13:287–289
- Duhamel G, Koubbi P, Ravier C (2000) Day and night mesopelagic fish assemblages off the Kerguelen Islands (Southern Ocean) *Polar Biol* 23:106–112
- Georges J-Y, Guinet C (2000) Maternal care in the subantarctic fur seals on Amsterdam Island. *Ecology* 81:295–308
- Georges J-Y, Bonadonna F, Guinet C (2000a) Foraging habitat and diving activity of lactating Subantarctic fur seals in relation to sea-surface temperatures at Amsterdam Island. *Mar Ecol Prog Ser* 196:279–290
- Georges J-Y, Tremblay Y, Guinet C (2000b) Seasonal diving behaviour in lactating subantarctic fur seals on Amsterdam Island. *Polar Biol* 23:59–69
- Goebel ME, Bengston JL, DeLong RL, Gentry RL, Loughlin TR (1991) Diving patterns and foraging locations of female Northern fur seals. *Fish Bull* 89:171–179
- Goebel ME, Costa DP, Crocker DE, Sterling JT, Demer DA (2000) Foraging ranges and dive patterns in relation to bathymetry and time-of-day of Antarctic fur seals, Cape Shirreff, Livingston Island. In: Davidson W, Howard-Williams C, Broady P (eds) Antarctic ecosystems: models for wider ecological understanding. New Zealand Natural Sciences, Christchurch, pp 47–50
- Goldsworthy SD, Hindell MA, Crowley HM (1997) Diet and diving behaviour of sympatric fur seals *Arctocephalus gazella* and *A. tropicalis* at Macquarie Island. In: Hindell M, Kemper C (eds) Marine mammal research in the Southern Hemisphere, vol 1. Status, ecology and medicine. Surrey Beatty, Chipping Norton, pp 151–163
- Green KG (1997) Diving behaviour of Antarctic fur seals *Arctocephalus gazella* Peters around Heard Island. In: Hindell M, Kemper C (eds) Marine mammal research in the Southern Hemisphere, vol 1. Status, ecology and medicine. Surrey Beatty, Chipping Norton, pp 97–104
- Green K, Williams R, Burton HR (1997) Foraging ecology of Antarctic fur seals *Arctocephalus gazella* Peters around Heard Island. In: Hindell M, Kemper C (eds) Marine mammal research in the Southern Hemisphere, vol 1. Status, ecology and medicine. Surrey Beatty, Chipping Norton, pp 105–113
- Guinet C, Cherel Y, Ridoux V, Jouventin P (1996) Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962–85. *Antarct Sci* 8:23–30
- Guinet C, Dubroca L, Lea M-A, Goldsworthy S, Cherel Y, Duhamel G, Bonadonna F, Donnay J-P (2001) Spatial distribution of the foraging activity of Antarctic fur seal *Arctocephalus gazella* females in relation to oceanographic factors: a scale dependant approach using geographic information systems. *Mar Ecol Prog Ser* 219:251–264
- Harcourt RG, Bradshaw CJA, Davis LS (in press) Summer foraging behaviour of a generalist predator, the New Zealand fur seal (*Arctocephalus forsteri*). *Wildl Res*
- Hindell MA, Slip DJ, Burton HR (1991) The diving behaviour of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia: Phocidae). *Aust J Zool* 39:595–619
- Kooyman GL (1989) Diverse divers: physiology and behaviour. In: Johansen K, Farner DS (eds) Zoophysiology series, 23. Springer, Berlin Heidelberg New York
- McCafferty DJ, Boyd IL, Walker TR, Taylor RI (1998) Foraging responses of Antarctic fur seals to changes in the marine environment. *Mar Ecol Prog Ser* 166:285–299
- Moore JK, Abbott MR, Richman JG (1999) Location and dynamics of the Antarctic Polar Front from satellite sea surface temperature data. *J Geophys Res* 104:3059–3073
- North AW (1996) Fish in the diet of Antarctic fur seals (*Arctocephalus gazella*) at South Georgia during winter and spring. *Antarct Sci* 8:155–160
- North AW, Croxall JP, Doidge DW (1983) Fish prey of the Antarctic fur seal *Arctocephalus gazella* at South Georgia. *BAS Bull* 61:27–37
- Orians GH, Pearson NE (1979) On the theory of Central Place Foraging. In: Horn DJ, Stairs ET, Mitchell RT (eds) Analysis of ecological system. Ohio State University Press, Columbus, pp 155–177
- Reid K (1995) The diet of Antarctic fur seals (*Arctocephalus gazella* Peters 1875) during winter at South Georgia. *Antarct Sci* 7:241–249
- Reid K, Arnould JPA (1996) The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. *Polar Biol* 16:105–114
- Rohlf FJ, Sokal R (1995) Statistical tables. Freeman, New York
- Sabourenkov EN (1991) Mesopelagic fish of the Southern Ocean – summary results of recent Soviet studies. *CCAMLR Sel Sci Pap* 1990:433–445
- Schreer JF, Testa JW (1996) Classification of Weddell seal diving behaviour. *Mar Mammal Sci* 12:227–250
- Sokal R, Rohlf FJ (1995) Biometry. Freeman, New York
- Swartzman G, Hunt G (2000) Spatial association between murrelets (*Uria* spp.), puffins (*Fratercula* spp.) and fish shoals near Pribilof Islands, Alaska. *Mar Ecol Prog Ser* 206:297–309
- Tabachnick BG, Fidell LS (1996) Using multivariate statistics. Harper Collins, New York