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Foraging routes of Antarctic fur seals (*Arctocephalus gazella*) investigated by the concurrent use of satellite tracking and time-depth recorders

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Abstract Little is known about movement behaviour in terms of route choice in Antarctic fur seals (*Arctocephalus gazella*). We deployed satellite transmitters and time-depth recorders simultaneously on 11 animals, and time-depth recorders with a speed recorder on 10 animals, to investigate the foraging routes of Antarctic fur seals belonging to a colony located at Iles Kerguelen (Southern Indian Ocean). The study took place during the 1997/1998 austral summer, and results indicate a preferred foraging area, with two main strategies in route choice apparent during foraging trips. In one strategy seals tended to reach an apparently known foraging ground and stopped there to feed. In the other strategy, animals performed looped trips, foraging en route and probably searching for a food patch better than the one previously exploited.

Introduction

In animals searching for food, foraging success may be related to different factors: the search method used in relation to the availability of prey and the spatial distribution of resources in the environment, ability in locating these resources, and the ability to adapt and to respond to environmental changes. If an animal adopts the strategy of central place foraging (Orians and Pearson 1979) during the breeding season these skills must be increased because in this case the resource found is,

directly (prey or regurgitation) or indirectly (milk), delivered to potential fitness (Stephens and Krebs 1986). In addition to the cost due to outbound and inbound trips from the resource patch, there are restrictions on the length of the trip. In many cases, offspring are less able than adults to compensate for different rates of energy intake and must be fed at regular intervals. For this reason, parents are restricted in their foraging range, and moreover, the food quality and quantity needed are increased. For example, lactating female seals need to consume 1.5–1.8 times as much food as non-lactating females (Perez and Mooney 1986; Costa 1991). Failure in locating a prey patch during a trip could be a waste of energy, the cost of which cannot be sustained, and could subsequently lead to breeding failure.

The foraging behaviour of some species of pinnipeds, such as fur seals during the pup-rearing period, can be defined as a central place foraging strategy. A fur seal female gives birth to a single pup and rears it during a period ranging from 4 to 36 months, while performing commuting trips to sea (Wartzok 1991).

Although many studies have previously described the foraging behaviour of fur seals, the majority have focused on diving behaviour and foraging effort during foraging trips (Gentry and Kooyman 1986; Kooyman and Gentry 1986; Costa 1988; Costa et al. 1989; Boyd et al. 1991, 1994; Boyd and Croxall 1992; Arnould et al. 1996; Boyd 1996). Few, to our knowledge, have investigated how these predators search their environment for prey in terms of route choice, considering the colony as the central place (Harcourt and Davis 1997; Boyd et al. 1998; Boyd 1999). The most complete method of studying a predator foraging at sea and diving under the surface is to track its route while simultaneously recording its diving behaviour (Loughlin et al. 1987; Goebel et al. 1991; Merrick et al. 1994; Campagna et al. 1995; McConnell and Fedak 1996; Harcourt and Davis 1997; Benvenuti et al. 1998; Francis et al. 1998). The lack of adequate technology has been the major reason for the difficulty in obtaining spatial data about the foraging trips of free-ranging animals. The development

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of satellite telemetry now enables the tracking of free-ranging seals equipped with satellite transmitters called platform terminal transmitters (PTT) (Stewart et al. 1989; Heide-Jørgensen et al. 1991; McConnell et al. 1992; Costa 1993).

Antarctic fur seals (*Arctocephalus gazella*) have been studied mainly at Bird Island, South Georgia, where they feed primarily on krill swarms during the breeding season (Croxall and Pilcher 1984; Doige and Croxall 1985; Reid and Arnould 1996). At this locality seals forage nocturnally for the most part, taking advantage of the diel pattern of krill migration to and from the surface (Croxall et al. 1985). Lactating females alternate, during a period of 4 months, trips to sea, with 1–2 days ashore to feed their pup. The trip to sea can be short (3–5 days) or long (6–8 days) (Boyd et al. 1991; Lunn et al. 1993). However, it is not clear if a short trip differs from a long one only in terms of days (a seal could remain longer at the same place) or also in terms of kilometres covered by the seal (Boyd 1999). This is due to the fact that most of the studies were carried out using time-depth recorders (TDR), a device that enables researchers to reconstruct the diving behaviour of the animal carrying it. In such a way it is possible to have an insight into the temporal behaviour of a seal during the foraging trip, but little can be inferred about the spatial behaviour of the seal. In the past, the problem with using external devices to study behaviour at sea has been that these devices caused an additional foraging cost to the seal due to drag, and they could modify the behaviour of the subject (Boyd et al. 1995, 1997; Walker and Boveng 1995; Francis et al. 1998). Improvement in microelectronic technology and a consequent reduction in the size of devices now means that more than one instrument can be deployed on the same subject, thereby enabling a more complete insight into the foraging behaviour at sea, and recording the route and diving behaviour simultaneously (Costa 1993; Harcourt and Davis 1997).

In order to investigate foraging routes of Antarctic fur seals at the Kerguelen Archipelago we equipped lactating females with both a PTT and a TDR. Nothing is known about the at-sea behaviour of this population, which does not feed on krill, but on myctophid fish (Cherel et al. 1997). Our report is the first attempt to study lactating females breeding at a colony at the Kerguelen Archipelago.

Materials and methods

Study site and device attachment

The study took place during the 1997/1998 austral summer in February and March. The study animals ($N = 23$) were lactating Antarctic fur seal females belonging to an increasing population at the Kerguelen Archipelago (Southern Indian Ocean). The colony is located on the northeast part of the main island, at Cape Noir (latitude 49.069°S, longitude 70.452°E), where approximately 400

females bred in 1998. Individuals were captured using a hoop net and restrained on a restraint board. Each seal was restrained for 10–20 min while the devices were attached. Two types of devices were deployed. The first, consisting of a time-depth recorder (Mk5-TDR Wildlife Computers, Redmond, Wash.) mounted on top of a platform terminal transmitter (Telonics ST10, packaged by Sirtrack, New Zealand) linked to the Argos system (Taillade 1993), was deployed on 13 animals. The package ($110 \times 42 \times 25$ mm, 150 g, cross-sectional area 10.5 cm^2) was shaped to decrease water drag. We deployed five PTT + TDR packages, three of which were deployed three times while the remaining two were deployed twice.

A Mk6 speed recorder (Mk6-TDR Wildlife Computers, Redmond, Wash., $80 \times 50 \times 50$ mm, 150 g, cross-sectional area 15 cm^2) was deployed on a second group of ten individuals in order to assess the speed of different events during foraging trips. The larger size of Mk6-TDRs precluded the simultaneous deployment of an additional PTT. We deployed each of the five Mk6-TDRs twice.

The devices were attached dorsally on the midline between the scapulae of each seal with double component araldite glue (AW 2101, Ciba Specialty Chemicals).

The colony was checked twice a day (at 0800–0900 hours and 1800–1900 hours) for returning seals. All the seals were recaptured after one foraging trip and packages were subsequently redeployed on different individuals.

Mk5-TDRs were programmed to record wet and dry periods and depth (metres) with a pre-calibrated pressure transducer every 5 s. Mk6-TDRs recorded speed (metres/second) with a rotating turbine, and depth (metres) every 5 s.

Satellite transmitter data treatment

Locations calculated in reference to three satellites were assigned by Argos to six classes on the basis of their estimated accuracy. The accuracy of locations provided by Argos is as follows: class 3 is accurate to 150 m, class 2 to 350 m, class 1 to 1 km, and class 0, A and B have no accuracy assigned. To assess the real error incurred by using different classes of locations we used locations recorded whilst the seals were known to be in the colony. Considering the distance between the central point of the colony (colony length: 500 m) and each actual location provided by Argos, we estimated a mean error of 524 ± 133 m ($N = 8$) class 3, 1399 ± 1293 m ($N = 27$) class 2, 1945 ± 1721 m ($N = 64$) class 1, 6184 ± 7552 m ($N = 47$) class 0, 4416 ± 5817 m ($N = 20$) class A, and $15,380 \pm 15,211$ m ($N = 15$) class B. However, this precision cannot be relied upon at sea as the number and quality of PTT messages received by satellites for each location and the travelling speed of seals could change during a foraging trip.

In order to evaluate if there were any differences during the day in the rate of location acquisition by satellites due to behaviour of seals (see Georges et al. 1997), we obtained the calendar of satellite passes during the study period in the study area (Argos Customer Service). This enabled us to calculate the theoretical distribution of locations obtained during the day. Theoretical and real distribution data obtained were then regrouped into 4-h time periods. In this way we obtained an easy separation between night and day, as the average values for sunrise and sunset during the study period were, respectively, at 0500 and at 2000 hours (local time).

Argos data were plotted using Elsa97 software (release 1.1, Soft & Technique Informatique) in conjunction with depth contour lines from GEBCO Digital Atlas (release 2, sheet 97.3).

Following the method of Boyd et al. (1998), we considered only the locations of the four best classes (Argos classes 0, 1, 2, 3) as, after a first analysis, most of the locations provided by classes A and B were clearly inconsistent with locations from other classes. Locations were filtered such that locations that required transit speeds greater than 3 m/s were discarded. The speed of 3 m/s was selected according to the Mk6-TDR speed. We determined this speed by grouping Mk6 speed readings into 0.5 m/s classes. Since

97.6% of readings lay between 0.5 m/s and 3 m/s, we considered that speeds higher than 3 m/sec could not be maintained for long periods by a seal. The route length was calculated by adding the segments of the broken line provided by plotting locations. The mean direction was calculated for each route as the mean vector of locations' bearing from the colony. The great circle distance to the furthest point from the colony reached was calculated using Elsa97 software.

Time-depth recorder data treatment

TDR records were used to estimate the duration of a foraging trip, and the foraging behaviour of seals in terms of how diving was organised during a foraging trip. Analysis of diving behaviour will be given in a separate paper.

We defined at sea activity in terms of periods of foraging activity and travelling or resting activity. The foraging periods are defined as those in which seals were active by diving, whereas travelling/resting periods are defined as the time with no dives or very scattered dives, in which seals presumably rested at the surface or moved between two different prey patches. The definition of the minimum criterion for the commencement of foraging activity during a foraging trip was a group of more than two dives deeper than 4 m occurring during a period of 15 min (Boyd et al. 1994; Boyd 1996). The dive record was searched sequentially from the start and once a grouping of dives had satisfied this criterion a search was made through the subsequent dives to find the end of the foraging activity. This was decided when an interval of more than 10 min occurred followed by less than three dives in 15 min. In this way isolated dives at the beginning and at the end of foraging activity were not included in a foraging activity event.

A movement index was defined, using Mk6-TDR speed data, in order to estimate the spatial displacement during foraging activity and travelling/resting events. The mean speed was calculated for each surface interval and multiplied for the duration of the interval (partial index). The movement index is the sum of all partial indices in one event. Incomplete events were excluded from calculation. The movement index does not take into account the possible horizontal distance covered during dives.

To compare the trip duration of equipped and non-equipped animals, we used a set of data recorded by direct observation of trip length (accurate to the nearest 0.5 days) during the study period (C. Guinet, M.A. Lea, S.D. Goldworthy, unpublished data). There was no apparent relationship between trip duration and time, in the short period in which the experiments took place. Subsequently one trip was randomly selected for each seal ($N = 78$) and used as the new data set.

Statistical methods

We used χ^2 and contrast tests (Neu et al. 1974) in order to evaluate differences between the theoretical distribution of locations and the actual distribution obtained.

A Mann-Whitney U -test was used to compare the trip duration of different groups and time spent travelling in different portions of the trip between groups.

Rayleigh and V -tests (Batschelet 1981) were used to test randomness in the mean directions of routes. The expected direction (45°), used to calculate the homeward component and V -test, is the mean bearing of a preferred foraging area determined by environmental factors like bathymetry and sea-surface temperature.

Hierarchical cluster analysis (HCA), using Ward's method (Ward 1963) and Euclidean distance, were used in order to evaluate the degree of similarity between routes. HCA was based on route length, mean direction, maximum distance from the colony and mean depth of locations as revealed by the GEBCO map, and was performed using Systat release 7.0.1 software package (Systat for Windows, SPSS).

Results

Movement behaviour

One of the 5 PTT units malfunctioned, resulting in the collection of spatial data for 11 individuals. The wet dry sensor (saltwater-switch) of the Mk5-TDRs recorded the departure and arrival times (both accurate to the nearest 5 s) of the 11 seals. A total of 519 locations were recorded at sea: 23% class A, 37.1% class B, 35% class 0, 4.9% class 1, 0.4% class 2 and 0.8% class 3. After filtering the locations as described in materials and methods, we obtained 178 locations, of which 83.5% were class 0, 12.1% class 1, 1.1% class 2 and 1.1% class 3. The frequency distribution of seal locations (from the non-filtered set) and the expected distribution calculated according to satellite passes during the PTTs presence at sea are given in Fig. 1. The observed distribution was significantly different from the expected one ($\chi^2_3 = 66.6$, $P < 0.001$). The contrast test ($P < 0.05$) shows that we obtained less locations in the hours of the night, as in two out of four classes (time period 5–8 and time period 13–16) more locations were obtained during the day.

The routes obtained for each seal are shown in Figs. 2 and 3 and data relevant to each route are given in Table 1.

With regard to the direction of the routes, we can divide them into three categories: five seals travelled northeast of Kerguelen and concentrated their activity in an area characterised by a rapid increase in bathymetry (Fig. 2b–f); another five seals concentrated their activity on a wide plateau of 500 m depth east/southeast of

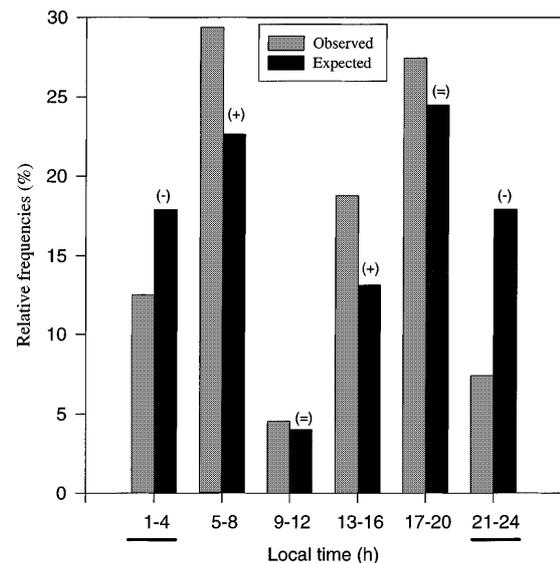


Fig. 1 Frequency distribution of locations calculated in accordance with satellite passes (black) and obtained by seals equipped with a PTT-TDR (grey) during 4-h periods. Night hours are shown by a black bar below; = indicates that the number of locations was equivalent to the expected value; - significantly less; + significantly more than the expected value (contrast test $P < 0.05$)

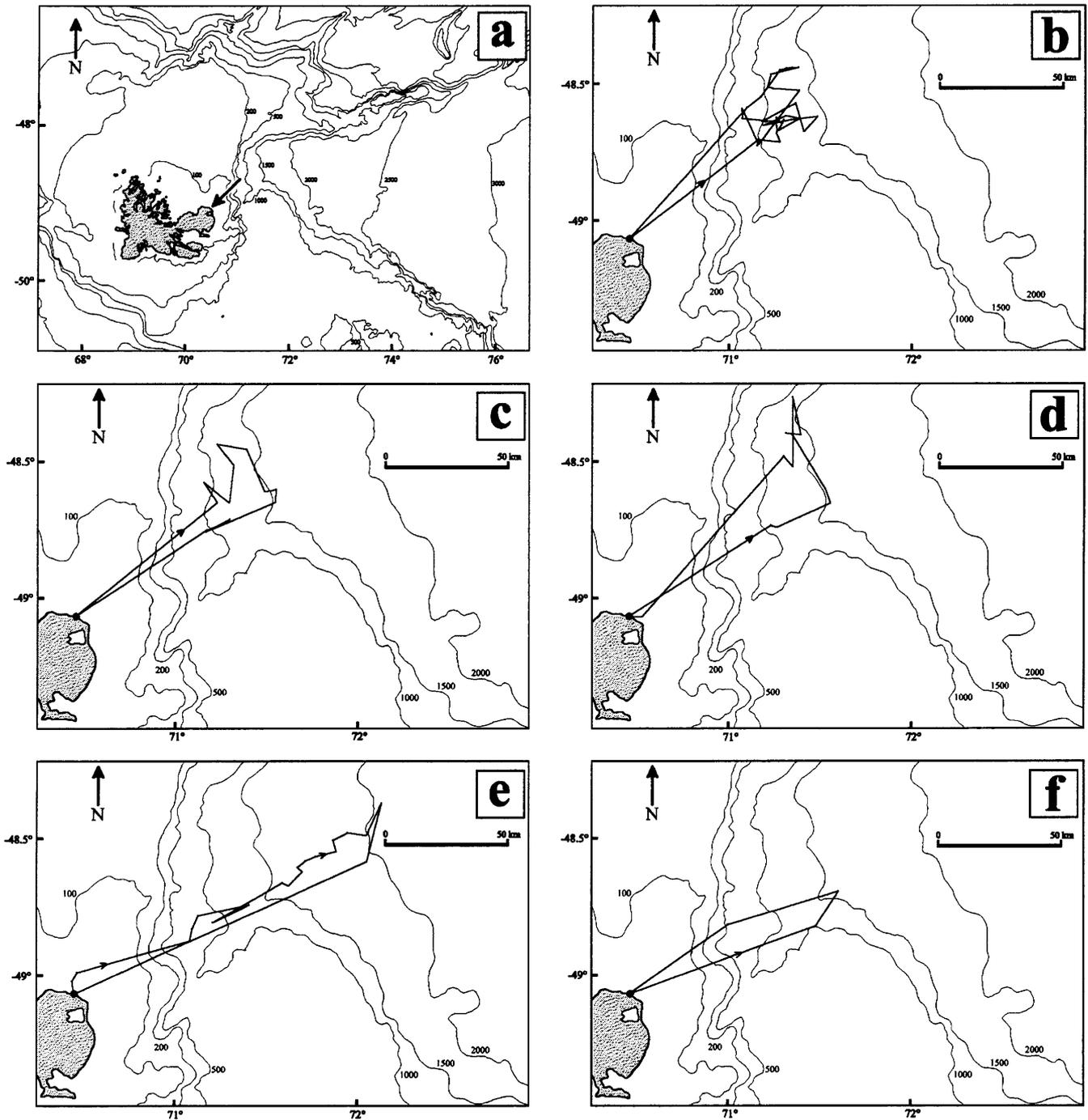


Fig. 2 a Map of the study area. Arrow indicates the location of the breeding colony, Cape Noir, at Kerguelen, and **b-f** (letters as in Table 1) five foraging routes of seals equipped with PTT-TDRs. A black spot indicates the breeding colony and arrows indicate the direction of route. Sea depth (m) is indicated by isometric lines

Kerguelen (Fig. 3g-i, l, n), and the remaining seal, m, made a trip that differed markedly both in terms of distance travelled and duration (Fig. 3m). The schematic representation of the clustering obtained with the HCA on route length, mean direction, maximum distance from the colony, and mean depth of locations (Fig. 4) shows the nodes separating the three main groups.

A first node (4.29) separates seal m from the others, and a second node (3.27) separates the other two groups.

For routes b, c, g, d, n and i, we can observe a concentration of locations in some part along the route. For seals b, c and d this concentration occurs in the same area. Seal m shows an initial orientation and a first concentration of locations similar to the routes bearing northeast, with a second concentration of locations occurring in the farthest area reached.

Rayleigh test and V -test show that mean directions of routes are not randomly distributed but are oriented toward the direction of a preferred foraging area (mean

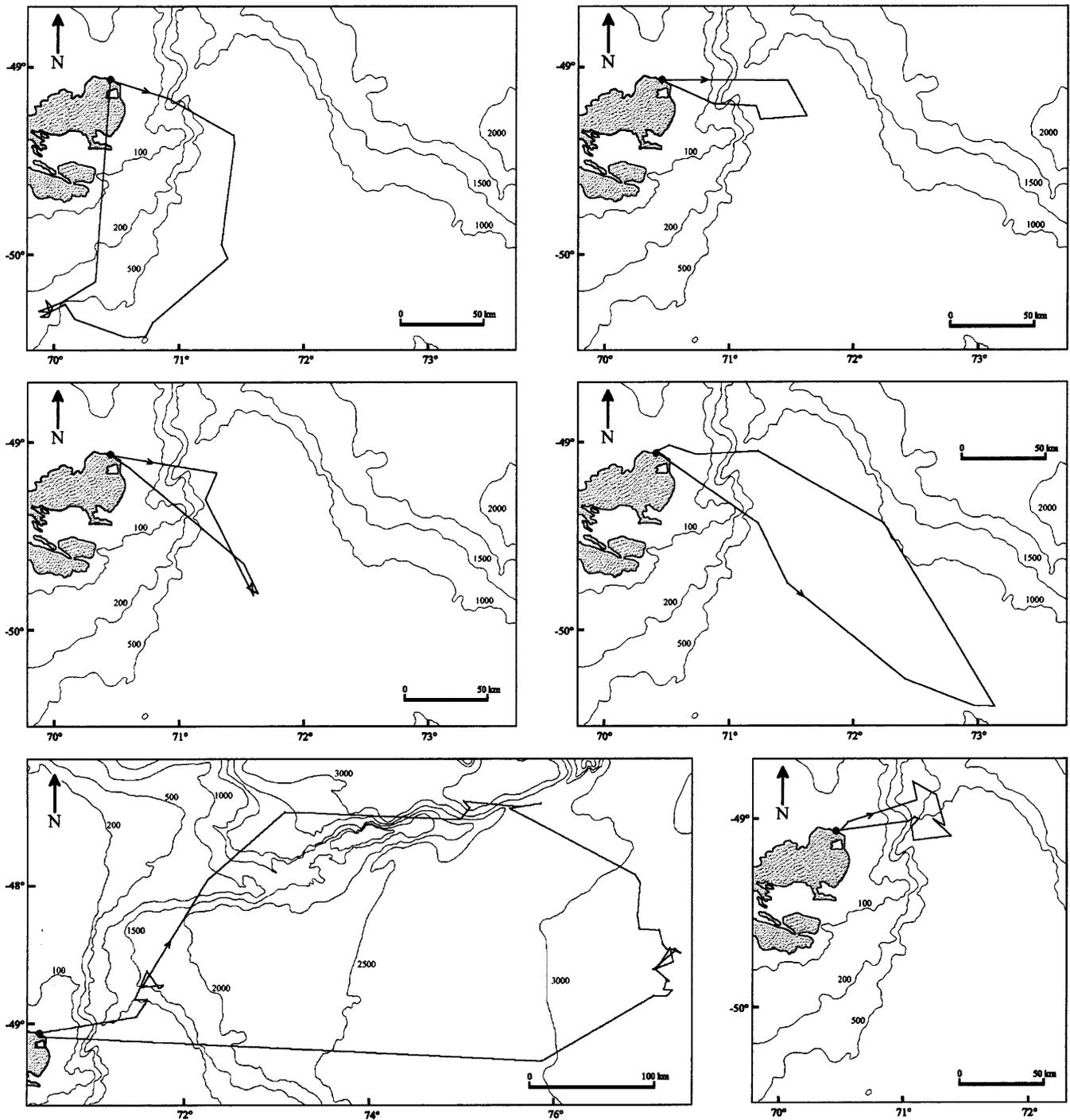


Fig. 3 Six foraging routes of seals equipped with PTT-TDRs (letters as in Table 1). A black spot indicates the breeding colony and arrows indicate the direction of route. Sea depth (m) is indicated by isometric lines

vector length = 0.8, direction = 82° and deviation from the expected direction = 37° ; Rayleigh test $P < 0.001$; homeward component = 0.64; V -test $P < 0.001$).

Time spent at sea, route length and maximum distance reached were positively correlated (respective Spearman rank correlation: $r_s = 0.917$, $N = 11$, $P < 0.001$; $r_s = 0.848$, $N = 11$, $P < 0.001$; $r_s = 0.890$, $N = 11$, $P < 0.001$).

The mean duration of foraging trips of seals carrying PTT/Mk5 was 7 ± 3.7 days ($N = 11$), and Mann-Whitney U -test showed no difference ($U = 561.5$, $N_1 = 78$, $N_2 = 11$, NS) between seals with and without equipment (\bar{X} : 8.2 ± 3.2 days, $N = 78$).

Diving behaviour

We recorded activity along the complete foraging route for 5 seals carrying a PTT/Mk5 out of 11. The devices

Table 1 Statistics for 11 foraging routes of PTT/Mk5-TDR equipped seals (times are given in local time). *Incomplete trip due to full memory of Mk5-TDR

Seal	Deployment time (date, time in hours) ^a	Trip duration (days)	No. locations	Mean direction ^b	Beeline distance (km) ^c	Route distance (km) ^d	Start time of first foraging activity (date, time in hours)	Outward trip duration ^e
b*	05/02, 1535	7.2	31	48(°)	98	404	06/02, 2027	4 h 52 min
c	05/02, 1620	5.7	13	52(°)	97	279	06/02, 2248	5 h 24 min
d*	12/02, 1603	5	11	51(°)	111	276	12/02, 2118	5 h 07 min
e	19/02, 1815	6.9	19	55(°)	145	365	21/02, 0003	9 h 15 min
f	25/02, 1232	5.9	3	63(°)	93	191	25/02, 2138	5 h 21 min
g*	05/02, 1714	8	19	172(°)	152	472	07/02, 2038	8 h 52 min
h	05/02, 1800	2.9	6	106(°)	88	192	08/02, 2028	7 h 29 min
i*	18/02, 1105	6.7	9	127(°)	118	281	19/02, 2135	6 h 09 min
l*	14/02, 1200	7.9	11	110(°)	243	525	14/02, 2031	4 h 30 min
m*	11/02, 1851	17	43	77(°)	547	1500	12/02, 1907	6 h 10 min
n	15/02, 1725	3.8	13	78(°)	68	206	16/02, 0031	6 h 59 min
$\bar{X} \pm SD$		7 ± 3.7	16.2 ± 11.6	$82(°)$	160 ± 136.8	426.4 ± 373.2		$6 \text{ h } 22 \text{ min} \pm 1 \text{ h } 35 \text{ min}$

^aTime at which the device was attached^bMean vector of locations' bearing from the colony location^cMaximum distance from the colony reached by a seal during a foraging trip^dTotal length of foraging trip^eTime elapsed between departure time and start time of first foraging activity event

deployed on the remaining six seals returned with full memories as they performed long foraging trips.

Data relative to each foraging trip are summarised in Table 1. Foraging activity events took place during the night, and seals were active each night throughout the trip. After the departure from the colony, seals travelled for a mean period of 6 h 22 min \pm 1 h 35 min (range: 4 h 30 min–9 h 15 min) before commencing a foraging activity event. Departure time and the time of the first foraging activity event were positively correlated (Spearman rank correlation: $r_s = 0.60$, $N = 11$, $P < 0.05$). The time spent travelling at a mean speed of 2.11 m/sec (calculated for the outbound trip from Mk6-TDR data) was sufficient for seals b, d and l to pass the

100-m depth contour, for seals c and f to pass the 200-m depth contour, and for seals g, h, m, n, i and e to pass the 500-m depth contour according to the direction of the first leg of the broken line representing the foraging trip.

Foraging activity events on subsequent nights commenced between 1747 and 2022 hours and ended between 0256 and 0808 hours in the morning. During some nights one or two pauses in foraging activity were longer than 20 min.

Speed analyses

Given the effect of Mk6-TDR on foraging trip duration of these seals, we have only considered relative speed between different activities. Complete TDR records were obtained for seven of ten seals carrying Mk6-TDR. The trip of seal p is almost complete as the device memory was full at 1148 hours and the seal was found at the colony at 1430 hours of the same day.

Data relative to each foraging trip are summarised in Table 2. The mean duration of foraging trips for seals carrying a Mk6-TDR was 11 ± 4.5 days and a Mann-Whitney U -test shows that a difference exists ($U = 542.5$, $N_1 = 78$, $N_2 = 10$, $P < 0.05$) between these seals and those without equipment (\bar{X} : 8.2 ± 3.2 days, $N = 78$). In addition, the durations of trips by seals carrying a Mk6-TDR were longer than those of seals carrying a Mk5-TDR and a PTT (Mann-Whitney U -test: $U = 86$, $N_1 = 10$, $N_2 = 11$, $P < 0.05$).

Foraging activity events took place during the night, and seals were active each night.

After the departure from the colony seals travelled for a mean of 6 h 35 min \pm 2 h 09 min (range 4 h 23 min–11 h 15 min) before starting the first foraging

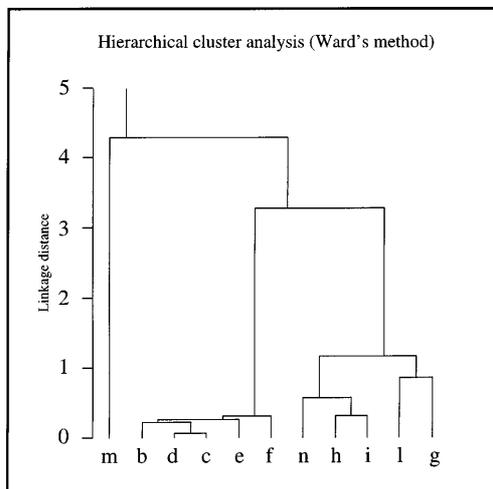


Fig. 4 Schematic representation of the clustering obtained by hierarchical cluster analysis on route length, mean direction, maximum distance from the colony and mean depth of locations (letters as in Table 1)

Table 2 Statistics for ten foraging trips of Mk6-TDR equipped seals (times are given in local time) (*incomplete trip due to full memory of Mk6-TDR; *MI* movement index)

Seal	Deployment time (date, time in hours) ^a	Trip duration (days)	Start time of first foraging activity (date, time in hours)	Outward trip duration (hours) ^b	MI outward trip ^c
o	06/02, 1356	3.3	07/02, 2228	4 h 35 min	36.45
p*	06/02, 1234	14	06/02, 2036	7 h 58 min	56.89
q	06/02, 1445	6.8	06/02, 2335	6 h 12 min	36.58
r	20/02, 1750	11.4	22/02, 2228	5 h 50 min	43.87
s	06/02, 1530	10.2	07/02, 0052	11 h 15 min	78.25
t*	11/02, 1815	18	12/02, 1925	4 h 23 min	25.29
u	21/02, 1600	7	23/02, 2102	5 h 46 min	33.18
v*	13/02, 1735	11.5	15/02, 2029	8 h 45 min	44.79
w	06/02, 1307	10.6	08/02, 0307	6 h 32 min	50.47
z*	19/02, 1016	16.9	20/02, 2116	4 h 42 min	45.90
$\bar{X} \pm SD$		11 ± 4.5		6 h 35 min ± 2 h 09 min	45.2 ± 14.7

^a Time at which the device was attached

^b Time elapsed between departure time and start time of first foraging activity event

^c Movement index between the colony and the first foraging activity event

activity event. A Mann-Whitney *U*-test applied to time travelled after departure by the group of seals carrying a PTT and TDR and by the group of seals carrying a Mk6-TDR shows no significant difference between groups ($U = 40$, $N_1 = 10$, $N_2 = 11$, NS). There is a positive correlation between the departure time and the start time of the first foraging activity event in this group (Spearman rank correlation: $r_s = 0.662$, $N = 10$, $P < 0.05$).

For all the seals the beginning of foraging activity for all the nights spent at sea, except the first one, was between 1447 and 2025 hours. Foraging activity events ended between 0334 and 0932 hours. Seals o and r spent the majority of the last night at sea travelling back to the colony after a brief period of diving at the beginning of the night (these two nights were not included in mean calculation for the end time of foraging activity events).

Considering the mean speed during different parts of the trip, speed during the first leg (colony to the first foraging activity event) and the last leg (last foraging activity event to colony) was always observed to be higher than the travelling/resting activity speed during the rest of the trip (Fig. 5). Moreover, in some cases, travelling/resting activity speed increased during the last days of the foraging trip.

A similar situation is evident for the movement index during travelling/resting activity events (Fig. 6). Nevertheless, in several instances, at the start of a trip, the index for the first travelling/resting activity event was lower than that for the following travelling/resting activity event (e.g. Fig. 6r, t, v, z). This also occurred at the end of some trips (e.g. Fig. 6p, r, w) and may be explained simply by the fact that these seals were travelling for a shorter period of time. During some foraging activity events we observed one or two stops longer than 20 min in foraging activity in which the speed was more than 2 m/s.

A positive correlation between number of kilometers travelled per travelling/resting activity event and trip duration was observed for complete trips (Spearman rank correlation: $r_s = 0.821$, $N = 7$, $P < 0.05$). In

contrast, there was no correlation between kilometres travelled per foraging activity event and trip duration (Spearman rank correlation: $r_s = 0.357$, $N = 7$, NS).

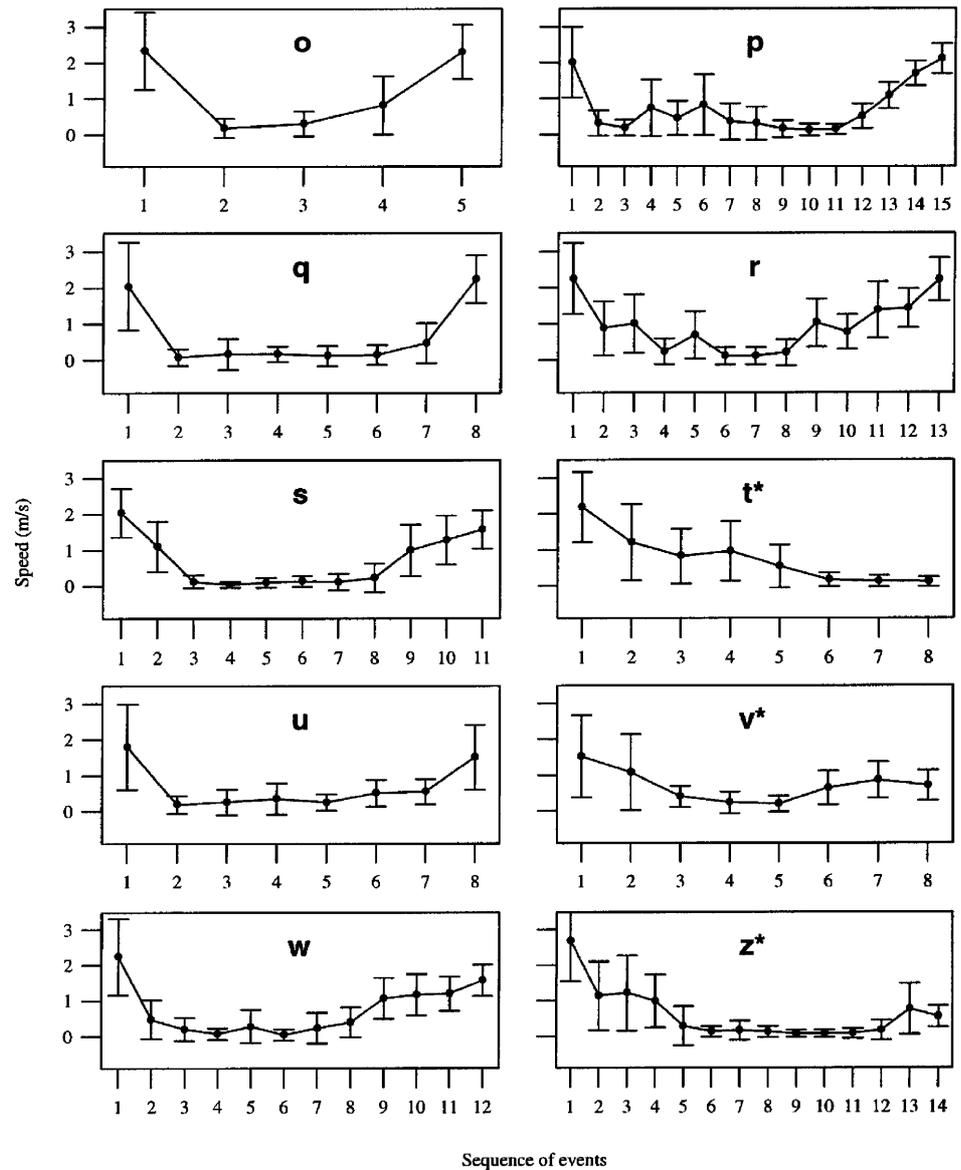
Discussion

An implicit difficulty related to the use of animal-borne devices is evaluating the effects of attaching the device, and the load and shape of the device, which may alter the animal's behaviour. In diving mammals the added frontal area of the device increases drag during both swimming and diving. The effect of an additional burden on the behaviour of fur seals has been taken into account in several papers. Boyd et al. (1991) concluded that Mk3-TDRs did not affect the foraging-attendance cycle of Antarctic fur seals. However, Walker and Boveng (1995) found differences in the average duration of foraging trips and periods ashore using the same device when compared to non-equipped seals. Significant differences in average duration of trips and in swimming speed were obtained using dummies simulating PTT (Boyd et al. 1997).

In this study, single Mk6-TDRs were deployed in one group, and a device package with dimensions comparable to the dummy used by Boyd et al. (1997) was deployed in the other. No difference was observed between foraging trip duration of PTT seals and those of unequipped seals. Moreover, in this group the duration of the trip, except for seal m, is within the upper range of trip duration obtained by other authors for the same species (Boyd et al. 1991; Lunn et al. 1993). This could indicate that the seals' behaviour, and therefore route choice, were mostly unaffected by the device package.

However, the foraging trips of animals carrying Mk6-TDRs were longer than trips of both PTT + TDR equipped seals and unequipped seals, indicating that this device can affect the seals' behaviour. Nevertheless, we can still infer important information about behaviour at sea.

Fig. 5 Mean speed (m/s) during consecutive travelling/resting activity events in seals equipped with Mk6-TDRs. Letters refer to Table 2; *incomplete record due to full memory



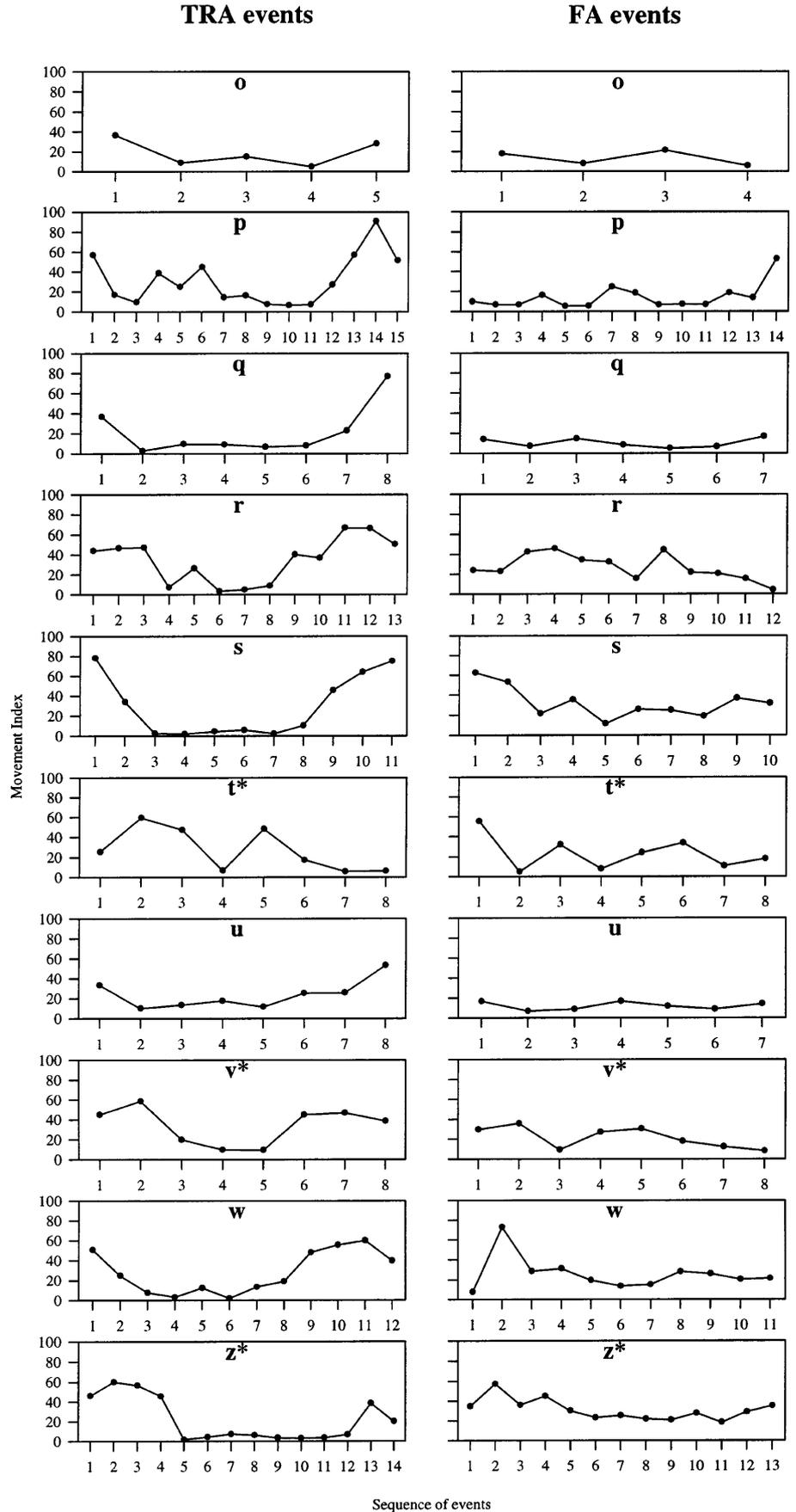
The use of circular statistics on foraging routes show that all seals travelled toward a preferred area, where they concentrated their activity, and that they were not dispersed around Kerguelen. Furthermore, we can observe two strategies in foraging trips. In one group, as indicated by a high concentration of satellite locations, seals concentrated their activity to the northeast of Kerguelen in a restricted area, characterised by a steep increase in depth. We can interpret the concentration of locations in two complementary ways. The first one is the more obvious and shows that a seal spent more time in a specific area. Secondly, a high concentration of locations is probably correlated with periods of resting behaviour during low movement travelling/resting activity events.

In fact, the observed frequency of locations is lower during the night and higher during the first part of the day when compared with the expected frequency. Resting probably occurs in the early morning, where low

speeds are generally observed, at the end of the night where all the foraging activity events took place. Therefore, the probability of obtaining a location is higher if the seal remains at the surface resting instead of travelling or foraging.

The Mk6-TDR speed data indicate that some seals travel more quickly during travelling/resting activity events at the beginning of the trip, more slowly in the middle and more quickly again at the end of the trip. This could be consistent with a behaviour of reaching an area at sea, fishing for some nights without moving during travelling/resting activity events and then returning to the colony. The route shape of animals included in the first strategy probably results from such a behaviour. In fact, the route shape shows an outbound and an inbound trip indicating that seals probably reach the feeding area directly from the colony and remain feeding in that area.

Fig. 6 Movement index in seals equipped with Mk6-TDRs during subsequent travelling/resting activity events (*left column*) and foraging activity events (*right column*). *Incomplete record due to full memory



In the second strategy, seals undertake longer looping trips on the Kerguelen plateau, fishing each night although probably searching for a good feeding ground. In fact, we observed a concentration of locations for seals *g* and *i* indicating a stay in a specific zone along the route, and perhaps indicating a good feeding ground located along the way.

The Mk6-TDR speed data further support this hypothesis. In some animals a high movement index is evident in most travelling/resting activity events of the trip, indicating that the seal was travelling during the majority of the trip between two areas of foraging activity. However, sometimes, not necessarily in the middle of the foraging trip, we can find one or more consecutive travelling/resting activity events with a low movement index, indicating that the seal stopped somewhere during the trip.

Since we have only one route per animal, we are unable to determine whether the two strategies are due to experience during preceding trips or to an individual tradition.

Seal *m* exhibited a different trip type and concentrated its activity (first locations concentration) in the same area as the group heading northeast, and afterwards continuing the journey to a region 547 km from the colony where a second concentration of locations occurred. In this case too, the trip appears to be input driven by, for example, prey abundance along the route, and it can therefore be included in the second strategy. Nevertheless, the distance from the colony reached and the areas in which the seal searched for food patches are different to most seals within the group.

All seals travelled a comparable number of hours before starting the first foraging activity event, and in some cases travelled during the first part of the first night at sea. This indicates that although seals usually feed each night, foraging activity is not started until a particular area is reached. A minimum depth before which it is not profitable to feed could represent the spatial limit. Apparently no seals fed before reaching the 100-m depth contour. It is not clear why some animals left the colony late in the evening using most of the first night to travel toward feeding grounds as the fishing activity primarily took place during the night. It could be due in part to the end of the suckling event, when all body reserves have been transferred to the pup.

During the longest trips, the movement index increased during the last three or four travelling/resting activity events when the seal was most probably en route to the colony. This could be related to the fact that seals that search for food along the way reach a further position from the colony than seals who go to a precise area, and thus they start to travel back, stopping during night to feed. The return trip generally took place during the day, after the last foraging activity event. In two cases the seal used the last night to travel back to the colony. This could be due either to prey patches of poor quality and/or to high motivation to return to fasting pups at the colony.

If we look at the movement index during the foraging activity, we must consider that the observed movement could be due to a repositioning behaviour between two dives. In this case we could consider the foraging activity event to be occurring in approximately the same spatial position. Nevertheless, during those nights in which we can observe stops longer than 20 min in duration, the movement index could indicate a change in prey patch with spatial displacement. Actually, during stops longer than 20 min the speed usually increased to 2–3 m/s, suggesting travelling behaviour. In this case a poor prey patch could lead to a recommencement of searching behaviour.

Arnould et al. (1996) found that seals undertaking short trips had a higher dive rate (m/h) than those undertaking long trips. They suggest that this is due to the fact that during short trips a seal expends less time in searching for food while seals undertaking long trips expend more time in searching but probably are better at exploiting food patches, or the quality of patches is higher.

Our findings seem to strengthen the idea that during longer trips seals do not stay longer in an area, but instead cover more kilometers probably searching for food. Firstly, there is a positive correlation between days at sea, kilometers travelled and maximum distance from the colony reached (PTT-TDR data) and secondly, there is a positive correlation between trip duration and kilometers travelled per day (Mk6-TDR data). Similarly, for the same species at South Georgia, Boyd (1999) found that the distance travelled during a foraging trip is positively related to foraging trip duration. The fact that a correlation does not exist between trip duration and kilometers covered per night means that during the night animals tend to feed and not to travel. Moreover, in seals undertaking long trips a longer stay in some areas, different from seal to seal and not necessarily related to the furthest area reached, seems to indicate the finding along a searching route of a good place in which to forage longer.

In conclusion, a double strategy of route choice seems to be present in this population of Antarctic fur seals. Further studies are required to assess these findings and to detect whether intra-individual differences in route choice exist between subsequent routes during the breeding period.

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