Movements and location at sea of South American sea lions (*Otaria flavescens*)

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Abstract

This study examined the foraging locations of lactating female and pre-breeding adult male South American sea lions *Otaria flavescens* in the Patagonian continental shelf, south-west Atlantic ocean. Research on females included the diving pattern, and was conducted during the 1994–98 breeding seasons in five northern and central Patagonian rookeries. Twenty females were satellite-tracked using the Argos system and yielded 1558 locations at sea. Satellite transmitters were also deployed on two adult males tracked for a total of 94 days ($n = 364$ locations) before the onset of the 1999 breeding season. Foraging trips for both sexes were confined to the temperate waters of the Patagonian continental shelf although males travelled greater distances than females, and arrived close (*c.* 80 km) to the edge of the shelf. Females from the same rookery dispersed widely and locations at sea often overlapped. Individual differences were apparent between coastal and pelagic animals. Trips lasted a mean of 3.4 days (SD = 1.3, $n = 115$ trips). Mean travel distance per trip was 206 km (SD = 117 km, maximum 864 km, $n = 115$ trips). Females reached further distances by travelling faster rather than by extending the duration of trips. Consistent with the shallow continental shelf, 65% of 75 087 dives recorded for nine animals were in the range of 2–30 m. Males alternated periods on the coast with trips to sea lasting a mean of 5.7 days (SD = 3.0, $n = 8$ trips). Mean travel distance exceeded 591 km (1 SD = 301 km, $n = 8$ trips). Results are consistent with sex differences reported from diet studies. Locations overlap with the summer operation of shelf fisheries targeting species that are also part of the sea lion diet.

Key words: *Otaria flavescens*, South American sea lions, diving, foraging behaviour, Patagonia

INTRODUCTION

The South American sea lion *Otaria flavescens* is one of the largest, most widely distributed and yet least studied of the otariids. About 68 000 animals (including pups) are grouped in 50 breeding rookeries and haul-out sites in northern and central Patagonia (Crespo & Pedraza, 1991; Dans *et al.*, 1996; Crespo *et al.*, 1997; Reyes, Crespo & Szapkievich, 1999). During the austral summer, adult females give birth to one pup, copulate about 1 week later and depart to sea, leaving their pup momentarily unattended (Campagna & Le Boeuf, 1988). Foraging trips 1–4 days long alternate with a similar period of nursing on land.

The diving behaviour of lactating female South American sea lions was described for animals from Península Valdés (Patagonia, Argentina; Werner & Campagna, 1995) and the Falkland (Malvinas) Islands (Thompson *et al.*, 1998). Foraging females from Patagonia perform short, flat-bottomed dives to median depths that varied among individuals from 19 to 62 m. They seem to be bottom and mid-water feeders that exploit a wide range of prey species in shallow waters. These results are consistent with diet studies (e.g. Crespo *et al.*, 1997; Koen Alonso *et al.*, 2000) and with reports from the Falkland Islands animals (Thompson *et al.*, 1998).

The distribution of dive depths suggests that lactating females remain on the shelf, close to the breeding sites. The mild slope of the shallow Patagonian continental shelf (< 100 m in most of its extension; Martos &

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Table 1. Summary of satellite tracking information for 20 lactating female *Otaria flavescens* from five breeding colonies and two adult males from Punta Norte rookery (Península Valdés). Calculations of mean distance travelled per trip, maximum distance from colony, median travel speed and minimum convex polygons (MCP) were restricted to complete trips as defined in Methods

Colony	Seal	Instrument deployed	Dives recorded	First location	Days to last location	Total locations	Locat. binded to trips	No. of trips	Mean ± SD duration (days)	Longest trip (days)	Mean ± SD time between trips (days)	Total travel distance (km)	Mean ± SD travel distance (km)	Max. travel distance (km)	Median speed (km/h)	Max. distance from colony (km)	MCP (km²)[a]
Females																	
Mte. Loayza	ML1	SDR-ST6	–	13 Jan 94	68	57	–	–	–	–	–	–	–	–	–	91	
45°09′S, 66°16′W	ML2	SDR-ST6	–	13 Jan 94	3	2	–	–	–	–	–	–	–	–	–	67	–
Punta Norte	N1	SDR-ST6	–	13 Jan 94	16	11	5	1	3.5	3.5	–	98	98	98	2.3	66	–
42°4′S,	N2	SDR-ST6	–	10 Jan 94	25	19	–	–	–	–	–	–	–	–	–	41	–
63°47′W	N3	SDR-ST6	–	04 Jan 95	11	4	–	–	–	–	–	–	–	–	–	113	
	N4	SDR-ST6	–	13 Jan 95	20	44	44	3	5.6 ± 1.5	7.8	1.3 ± 0.9	1333	444 ± 67	510	4.1	127	11 071
	N5	SDR-ST10	1281	09 Jan 96	19	52	47	2	6.9 ± 2.7	9.5	2.9	1048	524 ± 340	864	2.8	258	11 341
	N6	SDR-ST10	600	10 Jan 96	21	38	32	4	2.4 ± 0.3	2.8	1.5 ± 0.9	373	93 ± 14	106	2.4	50	637
Punta	BA1	SDR-ST10	–	14 Jan 96	3	5	–	–	–	–	–	–	–	–	–	19	
Buenos Aires	BA2	SDR-ST10	1243	20 Jan 96	6	18	11	1	3.3	3.3	–	281	281	281	3.9	122	–
42°14′S,	BA3	SDR-ST10	1116	09 Jan 96	6	16	12	1	3.2	3.2	–	105	105	105	1.9	38	–
64°22′W	BA4	ST10	NA	14 Jan 98	53	175	174	12	3.1 ± 0.4	4.2	1.4 ± 0.5	2381	198 ± 48	307	2.7	81	4407
Punta León	L1	SDR-ST10	14 745	10 Jan 97	77	195	186	15	3.4 ± 1.0	5.4	1.3 ± 0.5	2999	200 ± 65	318	2.8	152	7557
43°04′S,	L2	SDR-ST10	8045	15 Jan 97	59	69	65	11	3.5 ± 1.2	5.6	2.0 ± 1.8	2084	189 ± 71	266	3.2	147	7847
64°29′W	L3	SDR-ST10	9785	16 Jan 97	56	104	102	12	3.4 ± 0.6	4.3	1.1 ± 0.6	2882	240 ± 63	360	3.2	149	7718
	L4	SDR-ST10	17 258	14 Jan 97	71	180	174	14	3.9 ± 0.8	5.0	1.2 ± 0.5	4146	296 ± 81	400	3.8	173	17 054
	L5	SDR-ST10	21 016	13 Jan 97	71	232	229	16	3.5 ± 1.9	7.6	0.9 ± 0.8	2125	133 ± 73	249	1.8	105	2464
Punta	P1	ST10	NA	10 Jan 98	51	176	157	12	2.7 ± 0.7	3.8	1.2 ± 0.7	1341	112 ± 28	159	1.9	52	862
Pirámide	P2	ST10	NA	14 Jan 98	18	58	58	4	3.3 ± 0.8	4.2	1.4 ± 0.9	1350	338 ± 137	471	4.2	175	7210
42°35′S, 64°17′W	P3	ST10	NA	14 Jan 98	28	103	103	7	2.6 ± 0.3	3.1	1.4 ± 0.6	1112	159 ± 21	176	2.3	51	835
Total			75 089	–	682	1558	1399	115	3.4 ± 1.3	–	1.3 ± 1.0	–	206 ± 117	–	2.7	–	–
Males																	
Punta Norte–	Nm1	ST-18	–	14 Nov 99	53	196	174	4	5.5 ± 2.6	8.8	2.6 ± 1.5	2346	586 ± 268	862	5.2	285	9285
Punta Delgada	Nm2	ST-18	–	10 Nov 99	41	168	160	4	5.8 ± 3.3	8.9	1.9 ± 1.8	2974	595 ± 325	875	4.7	307	14 179
Total			–	–	94	364	334	8	5.7 ± 3.0	–	2.2 ± 1.7	–	591 ± 301	–	4.9	–	–

[a] MCP, minimum convex polygon. Only for individuals with > 30 uplinks.

Piccolo, 1988; Parker, Paterlini & Violante, 1997) precludes, however, determination of travel direction and location of potential foraging areas from data on dive depth. The location of potential foraging areas and the movements of individuals during foraging trips is not known for Patagonia, and was reported just for one individual from the Falkland Islands (Thompson *et al.*, 1998). The main purpose of this study was to detect shelf areas where females probably forage during early pup attendance, and to expand our understanding of the diving pattern. This paper also reports pilot work on movements at sea of pre-breeding adult males and describes sex differences in foraging behaviour.

METHODS

Study sites

Eighteen of 20 lactating females studied belonged to 4 northern Patagonia rookeries: Punta León, Punta Buenos Aires, Punta Norte, Punta Pirámide (Fig. 1, insets a–c, Table 1). Rookery refers to a pupping and breeding location. Punta León was the largest of the study sites, with about 2000 pups born per year. The rookery was located *c.* 60 km north of a fishing port (Rawson). The other 3 sites were located along the coast of Península Valdés. Punta Buenos Aires and Punta Norte were of similar size (*c.* 1300 pups born annually in each). Punta Buenos Aires occurred around a narrow and extended point that defines the eastern side of the mouth of Golfo San José. Punta Pirámide was the smallest of the northern Patagonian rookeries (*c.* 700 pups born per year). It was located on the coast of Golfo Nuevo, about 60 km from the city of Puerto Madryn. Additional work, involving the tracking of 2 lactating females, was conducted at Monte Loayza, a site located in central Patagonia, about 500 km south of Península Valdés (Fig. 1, Table 1). Monte Loayza was a haul-out (non-breeding) site for juveniles where about 200 breeding females congregated during the austral summer. The 2 adult males of this study were captured at Punta Norte (Fig. 2) where they returned to reproduce later in the season.

Study subjects and immobilization procedures

Adult females were captured during January 1994–98 (Table 1), 1–10 days after parturition. Body mass was estimated based on body size and on weights obtained during a previous study (Werner & Campagna, 1995). During the 1994–96 seasons, 11 females were immobilized using a combination of tiletamine HCL and zolazepam HCL (Telazol®). The dose of Telazol® (2.8 mg/kg estimated weight) was similar to that used by Loughlin & Spraker (1989) in northern (Steller's) sea lions *Eumetopias jubatus* and was given intramuscularly after restraining the animal in a net. During the 1997–98 seasons, 9 females were restrained in a net and

then immobilized with isoflurane gas (Ohmeda PPD, Inc., Liberty Corner, NJ, U.S.A.) via a face mask made from a rubber road cone, using a portable delivery system. Isoflurane field anaesthesia had previously been successfully used in field conditions with Steller sea lions (Heath *et al.*, 1996). We did not use, however, a combination of Telazol® and isoflurane gas as it was done with Steller sea lions. Atropine HCL (0.02 mg/kg estimated weight) was given intramuscularly 5 min before anaesthetic administration for 7 of the 12 animals which were to receive Telazol®, and for 5 of the animals receiving isoflurane gas, to reduce the risk of parasympathomimetic responses to the anaesthetics such as bradycardia and excessive salivation and mucus production. The dosage was derived from the standard pre-anaesthetic dosage of 0.02 mg/kg used for carnivores. Flumazenil (Mazicon®, Hoffmann-La Roche, Nutley, NJ, U.S.A.) was given intramuscularly at the end of procedures to females immobilized with Telazol®, using 1 mg of flumazenil for every 20–25 mg of zolazepam administered. Flumazenil reversed the centrally acting muscle relaxant effects of zolazepam that cause side-effects such as respiratory and cardiac depression.

Females were tagged with numbered colour tags (Allflex tags; Werner & Campagna, 1995) on the inner edge of front flippers to facilitate identification for observations of the attendance pattern. Pups were marked with a bleaching agent using numbers to allow individuals to be identified.

Males were captured at Punta Norte during the first week of November 1999, about 2 months before the onset of the breeding season (Campagna & Le Boeuf, 1988). Animals were immobilized with a combination of 250 mg tiletamine HCL and 250 mg zolazepam HCL (Telazol®) using a 3-ml plastic dart with a 60-mm needle to deliver the drug combination intramuscularly to a gluteal muscle (1.5 mg/kg estimated weight). Both animals were given intramuscular injections of flumazenil at the end of the handling procedures to reverse the effects of the zolazepam. Individuals normally recovered from anaesthesia within 1.5 h of darting.

Equipment and deployment

Sixteen of the 20 instruments deployed with females were microprocessor-controlled, satellite-linked, dive recorders (SDRs) that provided locations at sea and on land, and gathered data on diving behaviour (duration and depth). Locations were determined with the Argos satellite system (Service Argos, Inc., Toulouse, France and Landover, Maryland, U.S.A.). In 1994 and 1995, SDRs integrated a micro-processor controller (Wildlife Computers, Richmond, Washington) with a Telonics ST6, 0.5 W transmitter (SDR-ST6; approximate dimensions, $12.5 \times 5.2 \times 3.9$ cm; approximate weight, including glue, 400 g). In 1996 and 1997, smaller, quarter-watt instruments from the same manufacturer incorporated Telonics ST-10 transmitters (SDR-ST10;
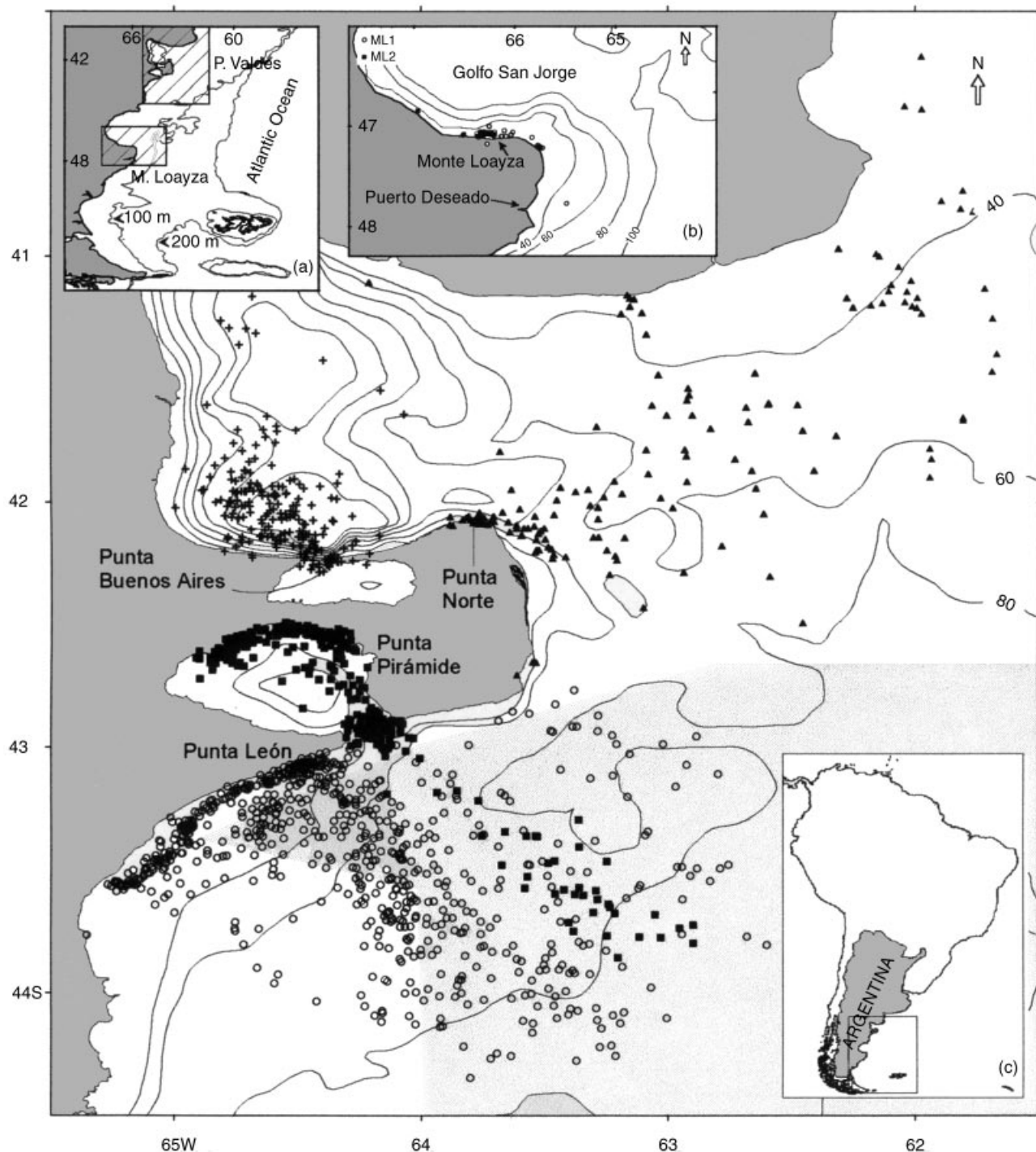
Fig. 1. Satellite locations at sea (*n* = 1558) obtained for 20 lactating female *Otaria flavescens* belonging to four breeding northern Patagonia rookeries (Punta Buenos Aires, Punta Norte, Punta Pirámide and Punta León). The shaded sector at sea overlapping with locations represents the main fishing area of the trawling fleet operating for hake *Merluccius hubbsi* in northern Patagonia during the summer (Crespo *et al.*, 1997). Insets (a)–(c): geographic location of study sites, with detailed reference to (a) northern and (b) central Patagonia rookeries. Rectangles in inset (a) show the approximate ocean range covered by locations in relation to the edge of the continental shelf (indicated by the 200-m depth contour).

approximate dimensions, 9.1 × 4.8 × 2.1 cm; approximate weight including glue, 200 g). In 1998, 4 platform transmitter terminals (PTTs; Telonics, Mesa, Arizona, U.S.A.) were used to determine geographic location. These PTTs did not sample diving data. SDR-ST6 units were glued to the back of the sea lions with marine epoxy (Evercoat Ten-set, Fibre-Evercoat Co., Cincinnati, Ohio, U.S.A.). SDR-ST10 and PTTs were glued to the top of the sea lion's head.

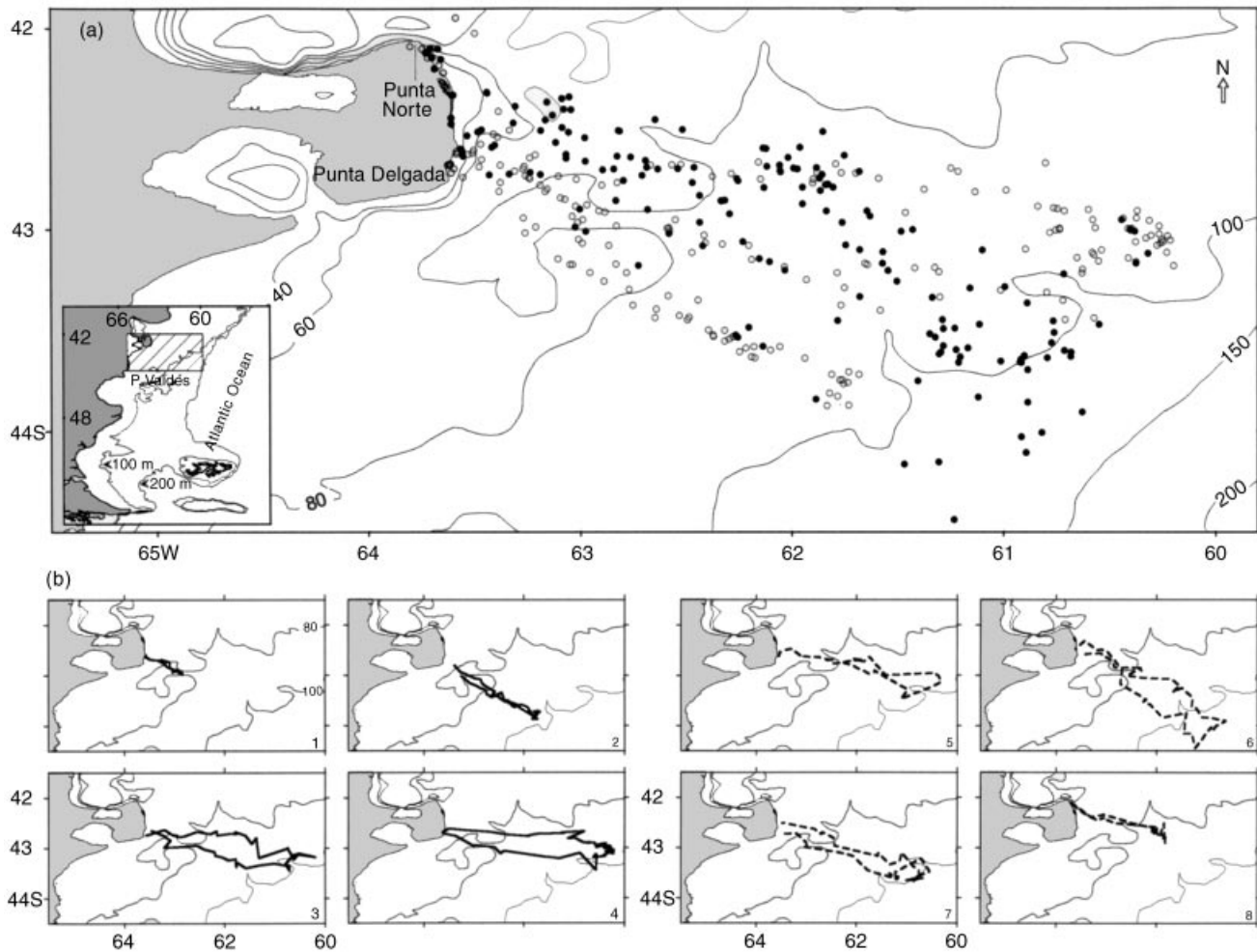Males were instrumented with ST-18 PTTs (Telonics,

Fig. 2. (a) Locations ($n = 364$) for two adult male *Otaria flavescens* (Nm1, open circles; Nm2, closed circles) instrumented at the rookery of Punta Norte (Península Valdés, Argentina) in November 1999 and before the onset of the breeding season. Inset: overall ocean area covered by male locations with reference to the 100 and 200 m depth contours. The 200-m contour indicates the edge of the continental shelf. (b) Details of trips by male Nm1 (b_{1-4}) and Nm2 (b_{5-8}).

0.5 W transmitters; Telonics, Mesa, Arizona; approximate dimensions, $9.1 \times 4.8 \times 2.1$ cm; approximate weight including glue, 200 g). These instruments did not sample diving data and were glued to the top of the sea lion's head using the method described for females.

Instrument programming and data analysis

SDRs used with females were programmed to transmit for 12 h, distributed throughout the day (00:00–01:00, 04:00–07:00, 09:00–12:00, 16:00–20:00, 22:00–23:00 GMT). Transmission hours were selected to fit satellite coverage and maximize battery life. Instruments had a salt-water switch to allow the transmission of signals only when animals were at the surface. Transmission rate was every 40 s at sea and every 90 s on land. Transmissions were suspended after 12 h on land.

Dive data were collected every 10 s and grouped into 3 different sets of histogram bins for dive depth, dive duration and time at depth. Only diving information gathered with ST-10 instruments during 1996 and 1997 were included in the analysis. Data were summarized as the number of dives (counts) in a histogram period of 6 h starting at 09:00, 15:00, 21:00 and 03:00 of local time (-3 h for GMT). The units measured dive depth from 0 to 235 m with a resolution of 1 m. We considered that the animal was in a dive any time that the instrument recorded a depth of >1 m. The upper limits of programmed dive-depth bins were 10, 30, 60, 90, 120 and >120 m. The upper limits of the dive duration bins were 1, 2, 3, 4, 6 and >6 min, and summarized the number of times the dive duration fell within each bin during the histogram period. For the purpose of representation in histograms, data were merged into 4 bins with upper limits: 2, 4, 6 and >6 min. Time at depth represents the fraction (%) of the 6-h period that the animal spent at each depth range. The upper limits of time-at-depth bins were 10, 30, 60, 90, 120 and >120 m. Dive information was stored in memory, thus data were not lost while the instruments were turned off between the hours when the instruments were pre-programmed to transmit.

Fixes were filtered following an algorithm that used a maximum swimming speed parameter of 2 ms^{-1}, as in McConnell, Chambers & Fedak (1992) and Thompson *et al.* (1998). Locations with a running mean speed greater than this value were rejected. Percentage of each Argos location quality category after filtering for 1558 locations was: classes 2 and 3, 7%; class 1, 17%; class 0, 40%; other, 36%.

Filtered locations were used to estimate distance away from Península Valdés, distance travelled and remote haul-out sites. Total distance travelled resulted from the interpolation of all filtered locations. The duration of trips and periods spent ashore were calculated based on departure and arrival from and to the rookery determined from fixes, diving data and direct observation of individuals. Calculations of mean distance travelled per trip, maximum distance from the coast and minimum convex polygon were restricted to complete trips (those
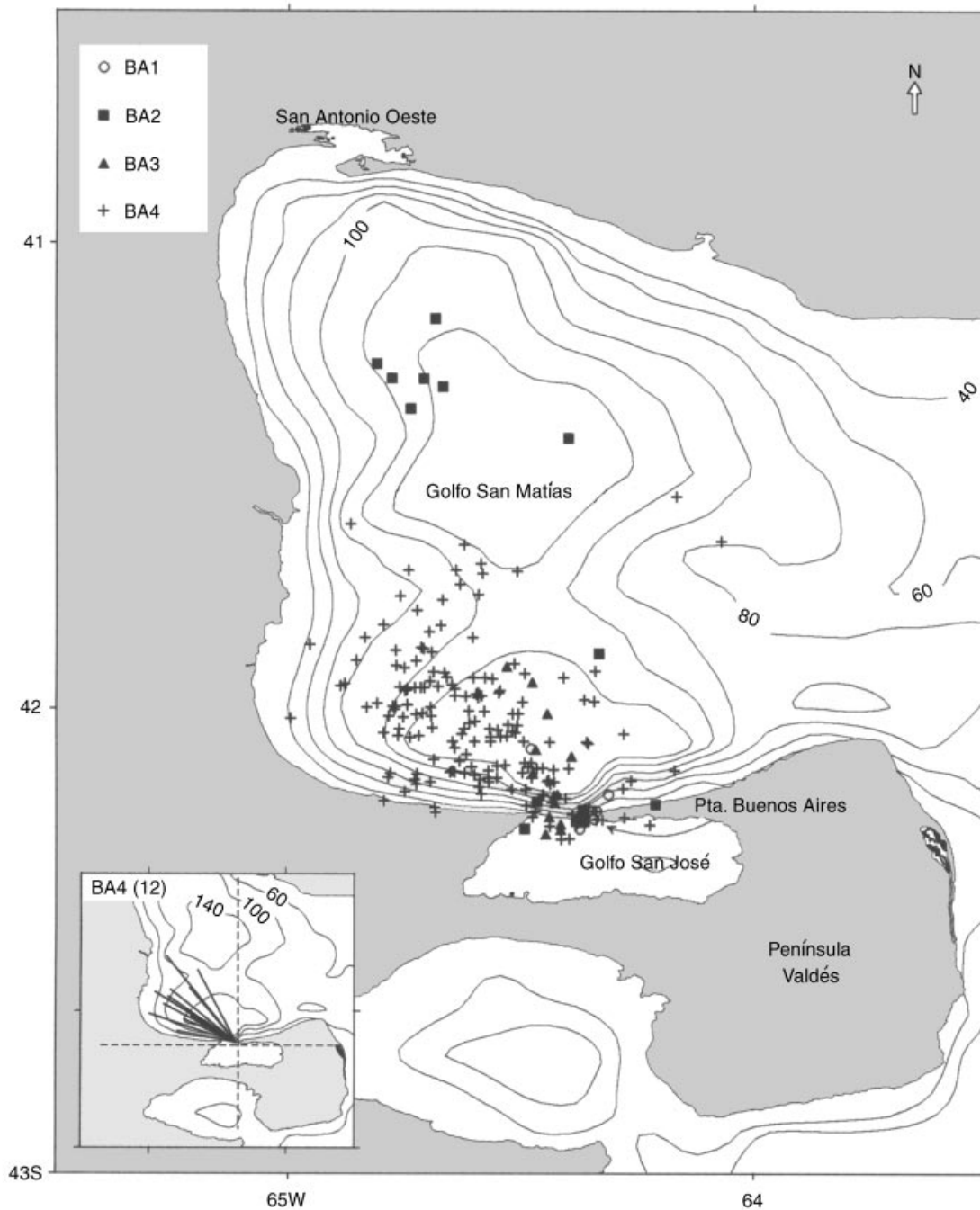

Fig. 3. Locations of four female *Otaria flavescens* from Punta Buenos Aires obtained during two seasons (1996, BA1-3; 1998, BA4). Most locations (81% of 214 data points) belong to one individual (BA4). The inner part of Golfo San Matías is one of the deepest sites of the Patagonian continental shelf (> 140 m). Inset: general travel direction for 12 trips of BA4 (lines range from pupping site to the furthest point reached).
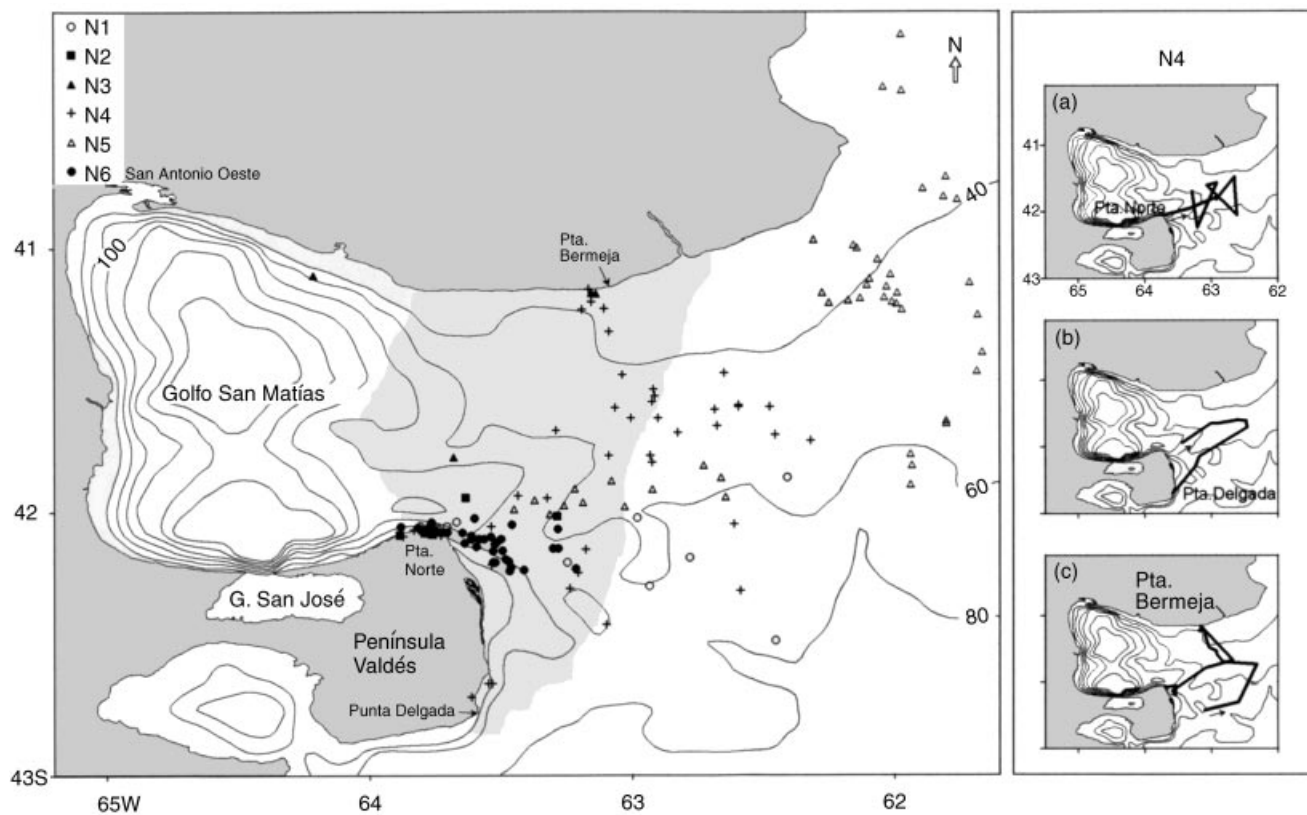
Fig. 4. Locations ($n = 168$) yielded by six female *Otaria flavescens* from Punta Norte studied during three breeding seasons (1994, N1 & N2; 1995, N3 & N4; 1996, N5 & N6). N3 and N4 hauled out near the rookery of Punta Bermeja. Inset: movements of N4 showing two haul-outs near (b)Punta Delgada and (c) Punta Bermeja rookeries.

circumscribed by locations at the rookery or within 10 km from it, while the animal was travelling towards the rookery). Locations for 5 animals did not show the complete trips. Locations from incomplete trips are represented in the figures but were not used in trip statistics shown in Table 1. Minimum convex polygons were calculated as the area enclosed by a line connecting the geographical extremes of the range of each animal. All trip variables derived from location data were analysed using custom software.

Male PTTs were programmed to transmit 19 h/day, distributed 10 h on, 3 h off, 9 h on, 2 h off beginning at 05:00 GMT, with a repetition rate of 45 s. Transmissions were suspended after 2 h out of water. Locations were determined with 3 Argos satellites. Percentage of each Argos location quality category after filtering for 364 locations was: classes 2 and 3, 8%; class 1, 21.7%; class 0, 43.4%; other, 26.9%.

RESULTS

Female trip duration, travel distance and travel speed

Twenty females yielded 1558 filtered locations, 83% of which were obtained for nine individuals instrumented in 1997 and 1998, from the four northern Patagonian rookeries (Table 1, Figs 1 & 3–6). SDR-ST6 that had to

be attached to the back of the animals yielded only 9% of the locations (Table 1). SDR-ST10 deployed in 1996 ceased transmission shortly after deployment because of a hardware failure. Complete foraging trips ($n = 115$ trips) were identified for 15 females and involved 90% of the filtered locations. Mean distance and time between interpolated locations were 10.5 km and 3.7 h, respectively. Seven animals were followed for 10 or more trips lasting a mean of 2.6–3.9 days each (Table 1). Attendance time on land was not correlated with the duration of the preceding and subsequent trips (Spearman rank order correlation, $P > 0.05$).

Trip duration correlated significantly with distance travelled (Spearman $r = 0.71$, $n = 115$ trips, $P < 0.01$) and, for some individuals (all Punta León animals, except L4) distance travelled increased as trips progressed (Fig. 7). Females apparently reached further distances by travelling faster rather than by extending the duration of foraging trips. Median travel speed between locations for all females was 2.7 km/h with individual differences ranging from 1.8 to 4.2 km/h (Table 1). The median travel speed between locations was significantly and positively correlated with mean travel distance per trip (Spearman $r = 0.79$, $P < 0.01$, $n = 15$ individuals), but was not correlated with trip duration (Spearman $r = 0.79$, $P > 0.05$, $n = 15$ individuals). Median speed was similar for the outgoing and incoming legs of the trips (2.5 *vs* 2.6 km/h calculated for 35 trips of eight females;
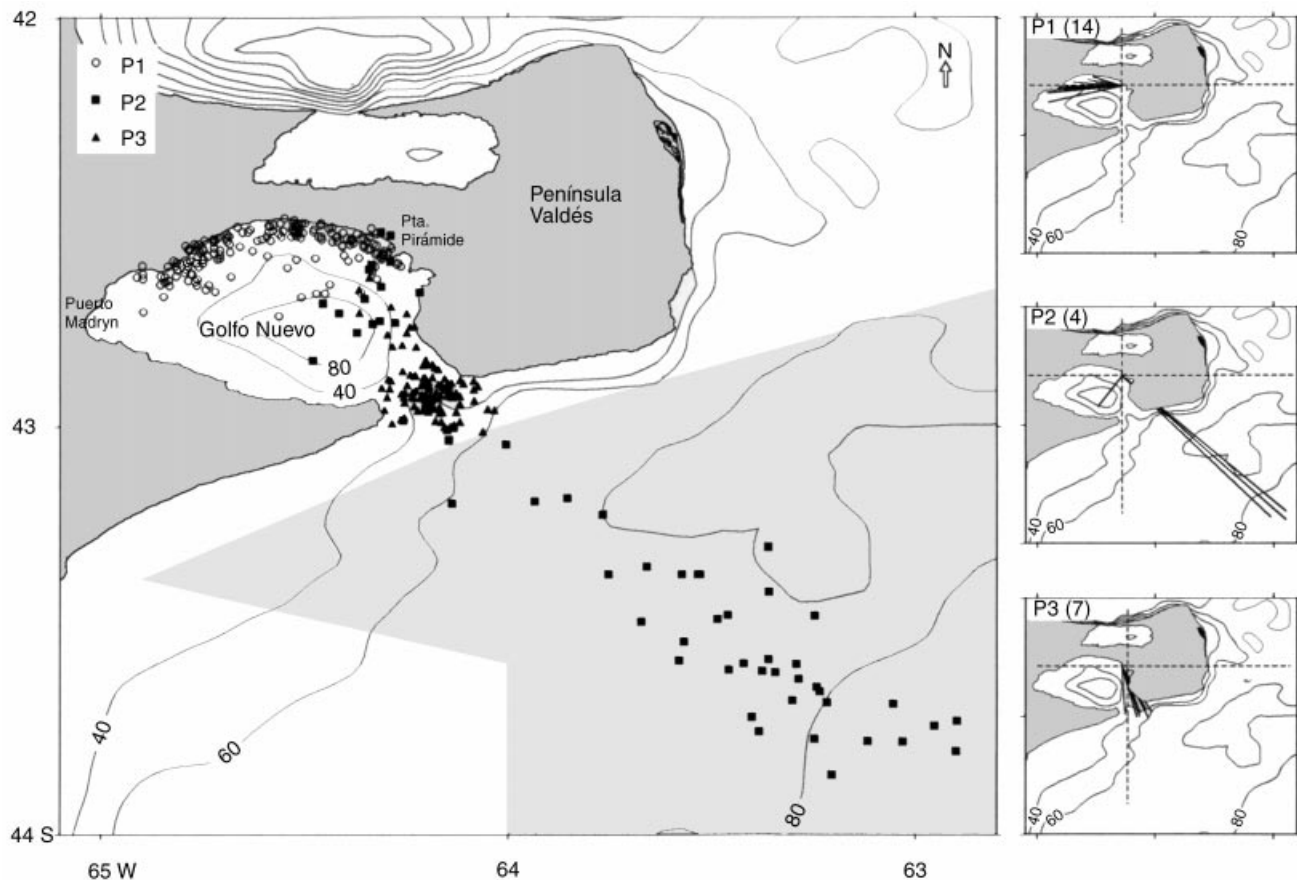
Fig. 5. Locations ($n = 337$) of three female *Otaria flavescens* from Punta Pirámide studied in 1998. Inset: general direction of travel based on 14, 4 and 7 trips for females P1, P2 and P3, respectively. Each line represents one trip connecting the rookery to the furthest location from it.

median test, $P > 0.05$). P2 was the fastest individual, travelling at a median speed that was almost 40% higher than the median for the entire sample.

Female locations and movements at sea

Foraging females remained within the limits of the continental shelf (indicated in Fig. 1 as the 200 m depth contour; rectangles of Fig. 1, inset a, show the geographic range of the locations in a larger scale). Northern Patagonia animals dispersed in a latitudinal range of about 4°. Straight-line distance between extreme locations at sea for these females was 486 km (compared to maximum distance of *c.* 100 km between Punta Norte and Punta León rookeries). Individuals of the same rookery differed in their pattern of movements at sea.

Punta Buenos Aires

Animals travelled out of Golfo San José but remained within the limits of Golfo San Matías (Fig. 3). BA4 (individual with the most extensive information for this site) travelled an estimated 2381 km in 12 trips. Her travel direction was consistently to the north-west of Punta Buenos Aires, reaching a maximum distance of

81 km from the rookery (Fig. 3 & inset; Table 1). She hauled out three times in three trips at a place about 30 km west of the departing rookery.

Punta Norte

Females travelled predominantly to the north-east (Fig. 4). The range of N5 was the most northerly and easterly of all the females studied (maximum distance from the rookery = 258 km). One of her trips lasted 9.5 days, during which she travelled at least 864 km with no recorded haul-out periods. Her long trips extended her home range to a minimum convex polygon of 11 341 km². Median travel speed for N5 was, however, similar to the overall median.

N4 had exceptionally long and complex trips. She hauled out twice during the same trip, in sites located > 70 km away from her rookery (Fig. 4a–c). After coming back from a trip that involved at least 472 km travelled in 4.3 days (Fig. 4a), N4 spent 2 days at Punta Norte and departed again (Fig. 4b). During this trip, she first spent 1.5 days ashore near or at the juvenile sea lion haul-out site of Punta Delgada. She then moved north-east, to a distance of 126 km off Punta Norte (Fig. 4c). Heading back, N4 made an abrupt change in
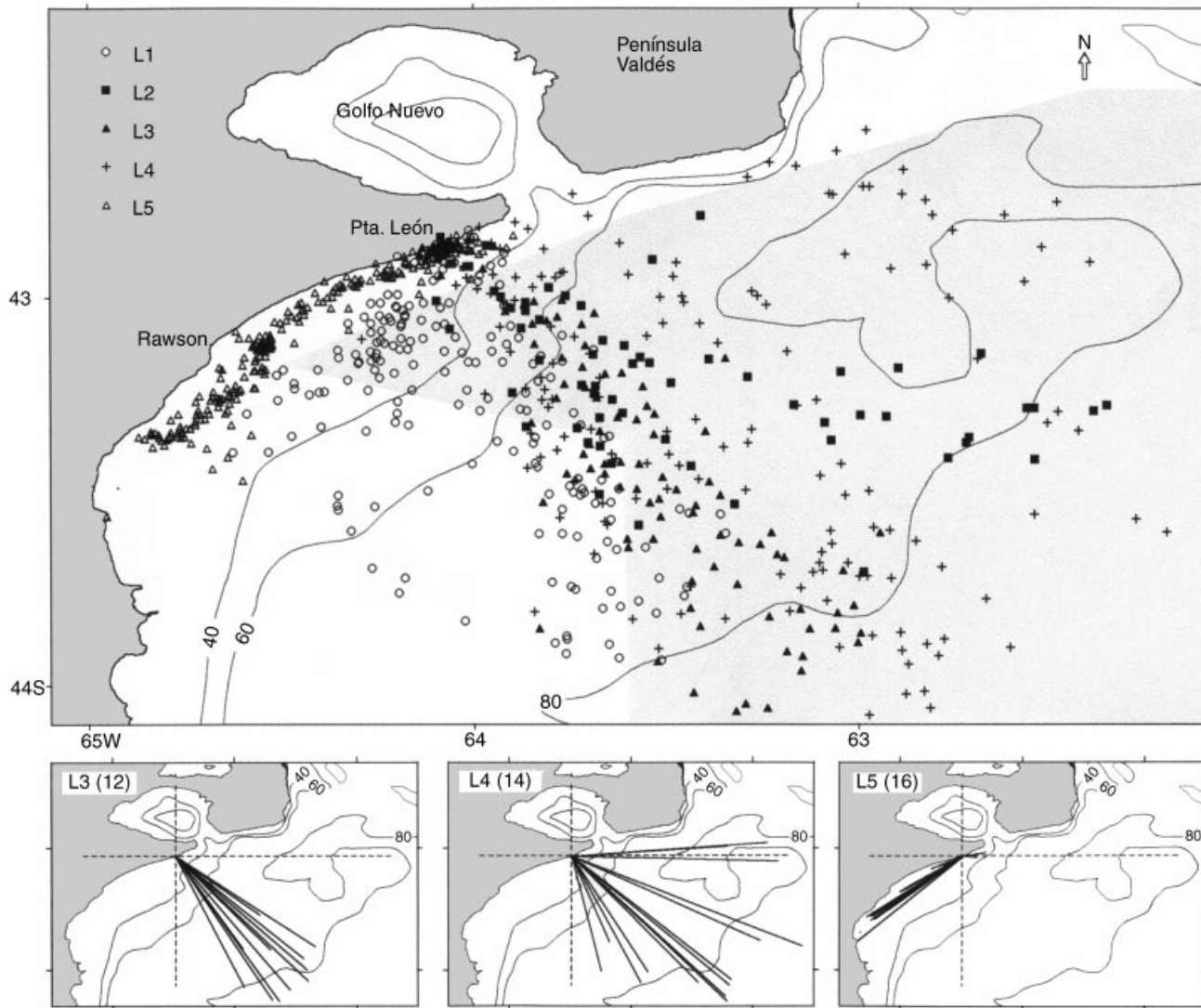
Fig. 6. Locations ($n = 780$) of five female *Otaria flavescens* from Punta León studied in 1997. The shaded sector at sea overlapping with locations represents the main fishing area of the trawling fleet operating for hake *Merluccius hubbsi* in northern Patagonia during the summer (Crespo *et al.*, 1997). The area south of Península Valdés, between the coast and the western limit of the shaded fishing sector represents a major early-summer, spawning place for Argentine hake (Ehrlich & de Ciechomsky, 1994). Insets: direction of travel for females L3, L4 and L5. Each line represents one trip connecting the rookery to the furthest site from it. Number of trips in parentheses.

direction to reach the northern coast of Golfo San Matías, where she hauled out near the rookery of Punta Bermeja. She finally returned to Punta Norte after a total of 12.5 days. Combined travel distance for both legs of her trip was 861 km. Her median travel speed was faster than that of most other individuals. N2 and N3 also hauled out in places away from Punta Norte. N3, like N5, came ashore near Punta Bermeja.

Punta Pirámide

P1 remained within Golfo Nuevo, consistently moving in all her trips along the northern coast of the gulf, apparently coming ashore several times at different sites

(Fig. 5 & insets). P2 made two complete long trips outside the gulf and contact was lost during her third trip. P3 travelled to the mouth of Golfo Nuevo without moving far into open shelf waters. She remained in an area of concentrated activity of about 200 km^2 with a mean depth of 40 m. She may have hauled out on both sides of the gulf mouth.

Punta León

Predominant travel direction was to the south-east of the rookery (Fig. 6) with mean travel distance per trip ranging from 133 to 296 km (maximum 400 km), Excursions lasted a mean of 3.5 days (SD = 1.2, $n = 68$
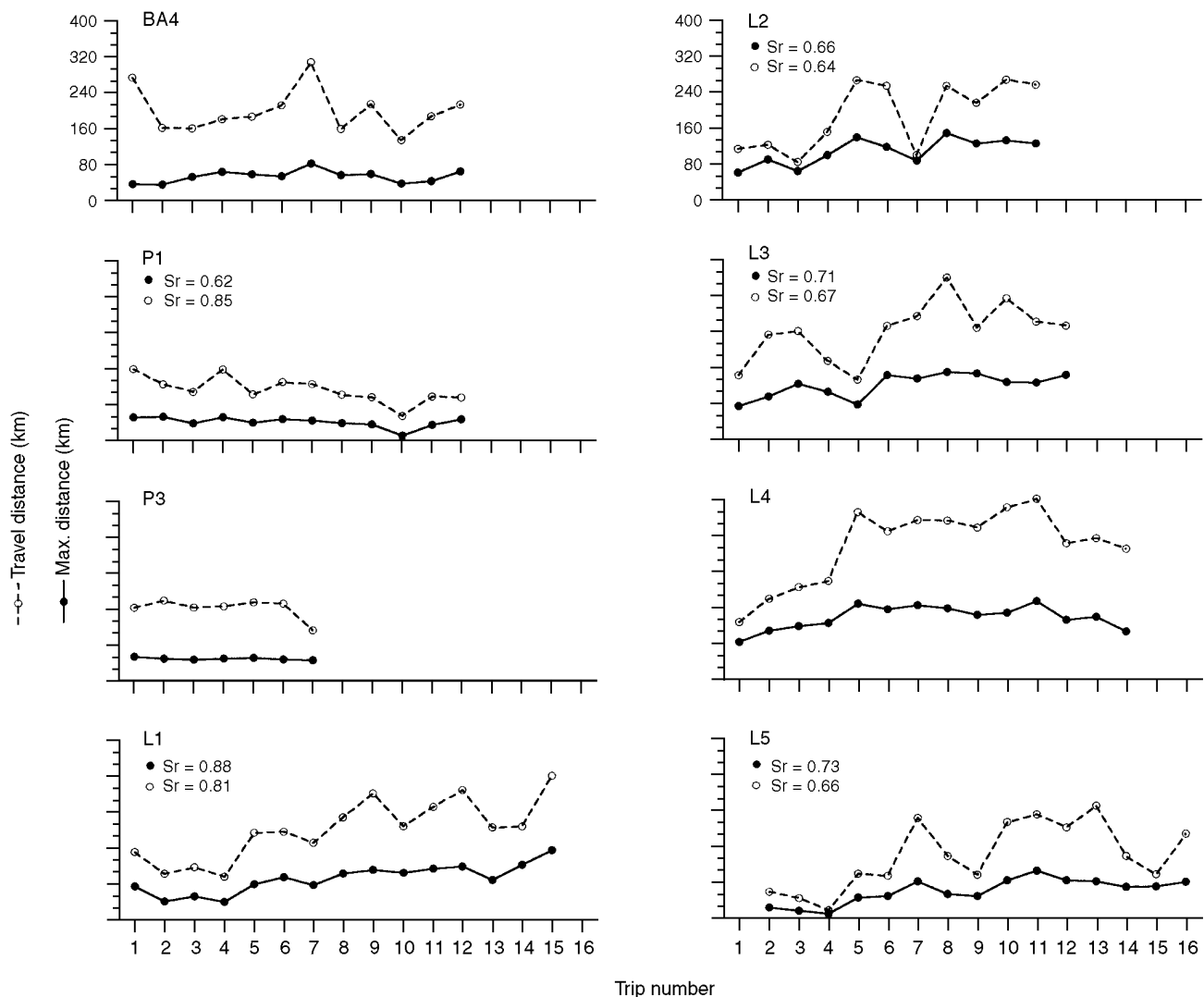
Fig. 7. Distance travelled and maximum distance to the rookery as a function of trip order. Each graph corresponds to a female *Otaria flavescens* with at least seven recorded trips. Travel distance and maximum distance to the rookery increased significantly ($P < 0.01$) with trip number for all Punta León females except L4 (Spearman rank order correlations; coefficient values in the figure). The correlation was in the opposite direction for P1, and it was not significant for BA4, P3 and L4.

trips). Three females travelled consistently to the open sea where their locations overlapped. None of them visited remote haul-out sites. L4 showed more variation in the direction of her trips than L2 and L3 (Fig. 6 insets). L5 remained in shallow waters, within 25–30 km off the coast. She interrupted her trips to haul out in several sites. L5 made trips along the coast spending time off the fishing port of Rawson (Fig. 6). L1 travelled predominantly to the open sea, with a few locations parallel to the coast.

Monte Loayza

One of the animals lost the transmitter soon after deployment and yielded a few locations for only 3 days. Data should be taken as preliminary for this rookery

and were virtually restricted to the coastal locations of ML1, all along the southern coast of Golfo San Jorge. Maximum distance from the rookery was 91 km (Fig. 1b).

Inter-rookery comparison

Locations of individuals from different rookeries rarely overlapped (Fig. 1). Exceptions were: P2 trips outside Golfo Nuevo to sites similar to those visited by L2 and L4 (Figs 5 & 6), N4 locations close to the northernmost areas visited by L4 (Figs 4 & 6), and N3 and N4 movements along the extended mouth of Golfo San Matías, partially overlapping with BA4 (Figs 3 & 4).

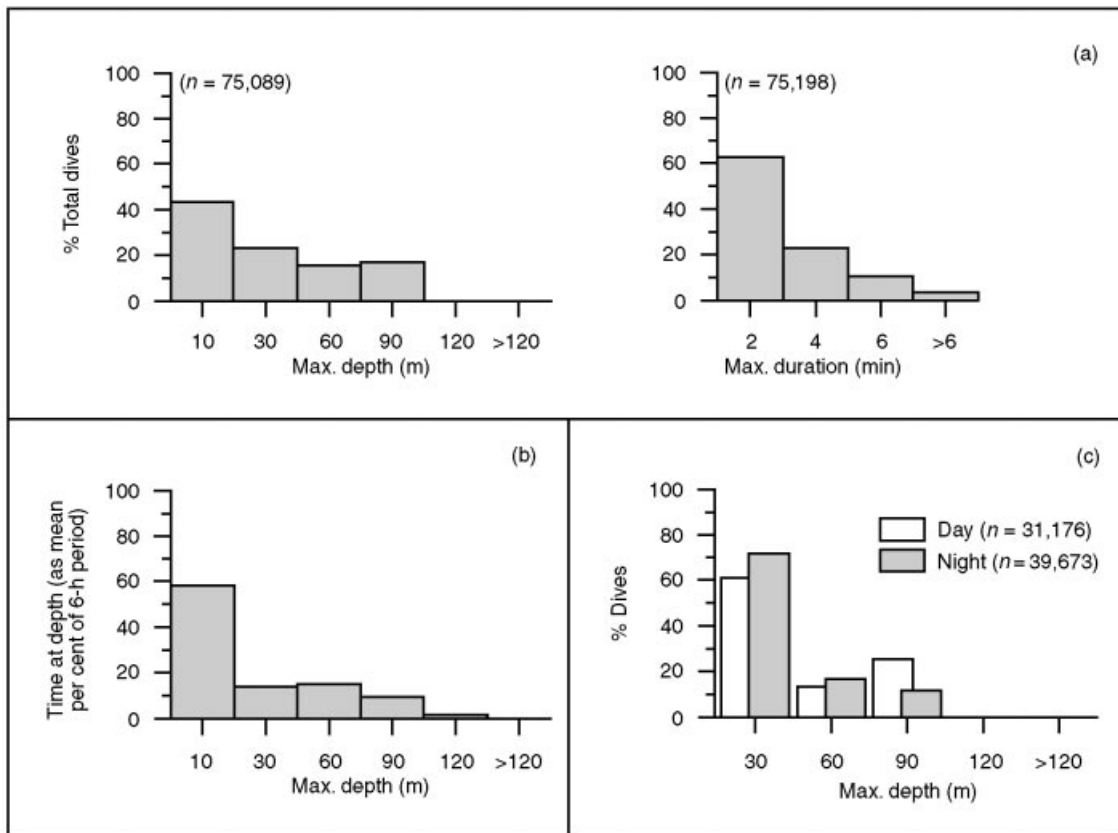Only P1 remained all the tracked time within Golfo Nuevo. P2 left Golfo Nuevo to the open sea and none

Fig. 8. Diving patterns of *Otaria flavescens*: (a) percentage distribution of dives (sample size in parentheses) for nine females as a function of depth and duration intervals; (b) distribution of the proportion of time under water spent at different depths expressed as the mean per cent time of 6-h periods for nine individuals; data for 521 periods of 6 h; (c) per cent dives (sample size in parentheses) for five depth classes during daylight (09:00–21:00) and predominantly night hours (21:00–09:00).

of the Punta León animals travelled inside the gulf, despite the relatively short distance between the latter and the breeding site. Likewise, all four females from Punta Buenos Aires rookery moved out of Golfo San José, and remained within the limits of the much larger, open and deeper Golfo San Matías.

Coastal females (P1 and L5) remained closer to their breeding site (52–105 km), travelled shorter distances (112–133 km per trip) and covered smaller ocean areas (862–2464 km^2) than more pelagic animals. Minimum convex polygon for L5 was three to seven times smaller than for the other four females from the same rookery, and dispersal area for P1 was the smallest recorded for females with at least 10 trips. Travel direction for P1 and L5 was consistent for all their trips (Figs 5 & 6). Both females travelled past and beyond fishing ports (Puerto Madryn for P1 and Rawson for L5).

Female diving pattern

Histograms transmitted were based on over 75 000 dives recorded for nine females from three rookeries in 1996 and 1997 (Table 1). Data for 1997 allowed a distribution of dive depth and duration as a function of local time in 6-h periods.

Dives were short and shallow; 85% lasted < 4 min, and 43.6 % were in the range of 2–10 m (Fig. 8a). Coastal females (e.g. L5) had preferred depths in the range of 10–30 m (65% of 21 016 dives); L5 never exceeded a depth of 60 m. Females that travelled > 100 km away from the rookery also had a high proportion of dives in the 2–10 m range of depths (61%, 47% and 57% for L2, L3 and L4, respectively). Six of nine females virtually never dove deeper than 90 m. Dives deeper than 90 m made < 1% of the sample. Most deep dives were performed by three individuals (N6, BA2 and BA3), two of which travelled inside Golfo San Matías, one of the deepest areas on the otherwise shallow shelf (Fig. 3). BA2 was exceptional in that 22% of her 1243 dives were deeper than 120 m. The deeper diving pattern of N6 and BA2 was associated with 20% of the dives longer than 6 min.

Consistent with the pattern of shallow dives, > 50% of the time underwater was spent at depths of 2–10 m (Fig. 8b). Dives occurred during day and night (Fig. 8c), with a larger proportion of the deep dives (> 60 m) occurring during periods that covered predominantly

daylight h (63% of 12 562 dives of >60 m recorded for L1–L4).

Male locations

A few days after instrument deployment, both individuals moved south to a haul-out site near Punta Delgada, about 70 km from Punta Norte. All subsequent trips to sea departed from the Punta Delgada area.

Males spent about 60% of the total study time travelling at sea. More than 90% of 364 filtered locations obtained during 94 days were associated with eight complete foraging trips and three partial or short trips (Table 1, Fig. 2). Trips to sea consisted of 4- to 9-day-long, eastward excursions of maximum distances from the rookery exceeding 300 km (Table 1, Fig. 2). Males arrived close (*c.* 80 km) to the 200 m depth contour that indicates the edge of the continental shelf (Parker *et al.*, 1997). Travel direction was similar during different trips and locations overlapped between the two individuals (Fig. 2b$_{1-8}$). By early January 2000, individuals returned to Punta Norte where they held harems, thus their trips to sea reflected the last foraging activity before a fasting period of about 2 months.

DISCUSSION

Female foraging behaviour

Lactating South American sea lion females from several northern Patagonia rookeries forage within the limits of the Patagonian continental shelf (Fig. 1). The rare overlap at sea of individuals from different rookeries suggests segregation of foraging areas of females during lactation.

Satellite-derived locations for female South American sea lions are available for comparative purposes for one lactating female from the Falkland Islands (Thompson *et al.*, 1998). The travel pattern of this individual combined extended trips, such as those of female N4 of this study, with shorter trips, such as those of L5 and P1. During short trips, most activity occurred in a small area, as described for P3. None of the Patagonian females remained so consistently close to the breeding site as the Falkland Island animal (mean maximum distance of 32 km).

Lactating females of the Antarctic fur seal *Arctocephalus gazella*, New Zealand fur seal *Arctocephalus forsteri*, Australian fur seal, *Arctocephalus pussilus doriferus*, Australian sea lion *Neophoca cinerea* and California sea lion *Zalophus californianus* also forage over the continental shelf or in relation to the edge of the shelf, close to the breeding sites (Harcourt *et al.*, 1995; Gales & Costa, 1997; Boyd *et al.*, 1998; Arnould, 1999; Sharon & DeLong, 1999). New Zealand fur seal females forage up to 78 km from the rookery, in waters shallower than the 200 m depth contour of the con-

tinental shelf and trips that last a mean of 3.3 days (Harcourt *et al.*, 1995). Exploitation of local resources during early lactation would be explained by restrictions in foraging range associated to the energetic requirements of pups (Boyd, McCafferty, Reid *et al.*, 1998). Adult females of the northern (Steller's) sea lion *Eumetopias jubata* with older dependent young increase their foraging effort and travel over larger home ranges than post-partum individuals (Merrick & Loughlin, 1997). Likewise, California sea lion females from San Miguel Island, California, remain on the continental shelf or edge of the shelf during the breeding season, but shift to more offshore locations later in the annual cycle (Sharon & DeLong, 1999). Occasional observations of South American sea lion females close to the edge of the shelf during late summer (J. F. Mermoz, pers. comm.) suggest that their foraging ranges may expand as pups become less dependent.

Location in relation to the productivity of the Patagonian shelf

The Patagonian shelf is a heterogeneous ecological system (Carreto *et al.*, 1986; Glorioso, 1987; Podestá, 1990, 1997). We attempted to relate sea lion locations with areas of differential productivity. Oceanographers described several sea fronts on the shelf, areas with enhanced vertical mixing resulting from strong tidal effects that create conditions of high productivity (Carreto *et al.*, 1986; Angelescu & Prenski, 1987; Glorioso, 1987; Podestá, 1990, 1997; Prenski & Angelescu, 1993; Olson *et al.*, 1994; Wilson *et al.*, 1995). Satellite imagery show that near-surface phytoplankton biomass on the shelf remains high throughout the austral summer (breeding season for South American sea lions) in areas that coincide with the description of tidal fronts (Podestá, 1990).

One of the most important sea fronts of northern Patagonia occurs at the mouth of Golfo San Matías (shaded area in Fig. 4), in the proximity of Punta Buenos Aires and Punta Norte (Carreto *et al.*, 1986; Glorioso, 1987; Glorioso & Simpson, 1994). Two summer spawning areas for Argentine hake *Merluccius hubbsi* occur in Golfo San Matías (Di Giácomo & Perier, 1992; Prenski & Angelescu, 1993) and south of Península Valdés (Podestá, 1990; Ehrilch & de Ciechomsky, 1994). Likewise, juveniles of the Argentine hake concentrate in Golfo San Matías and south of 43°S (Perez-Comas, 1990). These significant ecological areas of the shelf are accessible to sea lions from Punta Norte, Punta Buenos Aires and Punta León. At least one additional top predator of the shelf ecosystem, the Magellan penguins *Spheniscus magellanicus* from a colony located close to Punta Norte, forages close to the highly productive shelf fronts (Wilson *et al.*, 1995).

A much more productive area than tidal fronts occurs at the shelf break and extends along almost the entire length of the Patagonian shelf. The shelf-break front

supports a large biomass of fish, squid and top predators (Csirke, 1987; Rodhouse *et al.*, 1995; Rodhouse, Elvidge & Trathan, 2001). Several species of top predators forage along the edge of the shelf, such as southern elephant seals *Mirounga leonina* from Península Valdés (Campagna, Le Boeuf *et al.*, 1995; Campagna, Quintana *et al.*, 1998; Campagna, Fedak & McConnell, 1999), giant petrels *Macronectes giganteus* from near-shore islands located further south (F. Quintana & P. Dell'Arciprete, pers. comm.) and wandering albatrosses *Diomedea exulans* from the Island of South Georgia (Prince *et al.*, 1992). Despite the ecological importance of the shelf break, it seems to be inaccessible to lactating females constrained by pup demands to regularly return to land after relatively short periods at sea. At the latitude of Península Valdés, the continental shelf extends 300–400 km to the east before reaching the continental slope (Martos & Piccolo, 1988; Parker *et al.*, 1997). The extension represents three or more times the maximum travel distance from the rookery recorded for most females in this study. Male sea lions arrived closer to the edge of the shelf but did not rich it. Results then suggest that, at least during the summer, South American sea lions from northern Patagonia rely entirely on resources available within the Patagonian shelf ecosystem.

Female diving pattern

Previous findings describe lactating females from the Punta Norte rookery as both bottom and mid-water foragers (Werner & Campagna, 1995). Dive depth presented considerable individual variation and a bimodal distribution around 1–10 and 50–70 m. Most (69%) dives deeper than 10 m were flat-bottomed, U-shaped dives, suggesting benthic feeding. The rest of the dives were also U-shaped but showed vertical excursions at the bottom, suggesting mid-water diving. Dives did not have a diel variation in depth and frequency. Results from the present work are consistent with previous findings. Locations show that some females are predominantly coastal in their foraging habits, compatible with the shallow dives in the above mentioned bimodal distribution, while most pelagic individuals would explain the deeper dives.

Lactating females of the Australian sea lion, a species slightly smaller than the South American sea lion, would feed predominantly on the bottom, at mean depths of 67 m (Gales & Costa, 1997). Females of most other otariids are predominantly shallow, mid-water feeders (e.g. Gentry & Kooyman, 1986; Sinclair, Loughlin & Pearcy, 1994; Georges, Tremblay & Guinet, 2000). The large proportion of dives in the range of 2–30 m found in this study (Fig. 8a), the locations of individuals over the shelf and the associated bathymetry suggest that mid-water feeding may have been common in all study subjects. The depth range of the deepest dives (> 60 m) was similar to the depth of the shelf where most offshore locations occurred, thus some dives

of the most pelagic females may have reached the bottom of the shelf. Female New Zealand sea lions *Phocarctos hookeri*, not limited in the depth of their dives by a shallow shelf, dive to median depths of 124 m and reach maximum depths of 474 m (Gales & Mattlin, 1997).

Male foraging behaviour

Males remain on the Patagonian continental shelf, most of the time over waters shallower than 100 m. Although their foraging trips were longer than those of lactating females, males alternated relatively short periods at sea with time ashore. Data for pre-breeding Australian fur seals, show that females are capable of undertaking prolonged foraging trips of about 48 days before the pupping season (Arnould, 1999). These long trips are possibly related to the need to feed extensively to meet the energetic demands of late gestation. Although male South American sea lions may fast for > 2 months during the breeding season (Campagna & Le Boeuf, 1988), they would cope with the energetic demands of reproduction without having to spend extensive periods at sea during pre-breeding trips.

Behavioural comparisons with males of other otariid species are limited to a few studies, mostly of fur seals. Satellite tracking of pre-breeding male Australian fur seals *A. pusillus doriferus* show that animals also remain on the continental shelf between southern Australia and Tasmania, usually over waters shallower than 100 m (R. Kirkwood, pers. comm.). The same study showed that trips last about 8 days, during which males travel 200–400 km from their colony (occasionally over 600 km), and alternate with periods ashore of about 3 days. A translocation study with a non-breeding male Australian fur seal instrumented with a geolocation-time-depth also found that the animal spent most time over the shallow shelf waters (Hindell & Pemberton, 1997). Other studies involve post-breeding males. Two Antarctic fur seal males from the Island of South Georgia travelled in the direction of South Orkney Islands, and one reached Signy Island, a distance of about 900 km from South Georgia (Boyd, McCafferty, Reid *et al.*, 1998). Free-ranging adult male northern fur seals *Callorhinus ursinus* from rookeries in the Bering Sea and North Pacific Ocean move off the shelf into deep water during their post-breeding foraging trip, but tended not to go as far south on their migration into the North Pacific as females (Loughlin *et al.*, 1999, pers. comm.). The only sea lion species for which comparative data on male behaviour are available is the Australian sea lion. Breeding males of this species from Kangaroo Island dive deeper than females and apparently reach the edge of the continental shelf (N. J. Gales & D. P. Costa, pers. comm.).

Diving data are not available for South American sea lion males. However, as our study subjects remained on the continental shelf, their maximum dive depth, as that of females, would have been restricted by the depth of

the shelf. It is thus expected that most dives were relatively shallow for a large sea lion. Based on bathymetric data, *c.* 90% of the satellite locations coincided with areas 50–100 m deep.

Sex differences

Free from reproductive constraints, pre-breeding males travelled about twice as far east and to deeper waters than lactating females. Distinct foraging locations are consistent with sex differences reported in diet studies based on stomach contents of adult sea lions from northern and central Patagonia. The description of the diet suggests that females have coastal and benthic predation habits, whereas males are more pelagic and prey in the water column (Crespo *et al.*, 1997; Koen Alonso *et al.*, 2000). The main prey for females is the red octopus *Enteroctopus magalocyathus* followed by Argentine shortfin squid *Illex argentinus*. Males would forage mainly on Argentine hake and Patagonian squid *Loligo gahi* (Crespo *et al.*, 1997; Koen Alonso *et al.*, 2000).

Sex differences in foraging locations of adult otariid males and females were also reported for the Antarctic fur seal from the Island of South Georgia (Boyd, McCafferty, Reid *et al.*, 1998). Post-breeding male Antarctic fur seals dive deeper and migrate further away and to different geographical areas than females with pups. While the latter travelled north-west of the island and remained mostly over its continental shelf, males move south, towards the Antarctic Peninsula (Boyd, McCafferty, Reid *et al.*, 1998). These results on fur seals are similar to our findings, although sea lion males were in the pre-breeding phase of the annual cycle.

Interaction with fisheries

Data on diet, locations of potential sea lion foraging areas in relation to fisheries operating on the shelf, and the present impact of fisheries on the ecology of the Patagonian shelf (evidenced by the recent collapse of the Argentine hake fishery), suggest that shelf fisheries may create sub-optimal foraging conditions for breeding sea lion females. Two of the most important prey items of the sea lion diet (Argentine hake and shortfin squid; Crespo *et al.*, 1997; Koen Alonso *et al.*, 2000) are also the major targets of fisheries that operate on the continental shelf and along the edge of the shelf (Perez-Comas, 1990; Podestá, 1990; Rodhouse, Barton *et al.*, 1995; Crespo *et al.*, 1997; Haimovici *et al.*, 1998; FAO, 2000; Rodhouse, Elvidge *et al.*, 2001). These commercially valuable species were exploited most heavily from the mid-1980s and throughout the 1990s, when more vessels were incorporated and the fishing areas expanded (Csirke, 1987; Prenski & Angelescu, 1993; Bezzi *et al.*, 1994; Crespo *et al.*, 1997; FAO, 2000). Since then, the Argentine hake fishery collapsed and the squid fisheries expanded (FAO, 1999).

Female locations at sea overlap with the most important fishing grounds and the highest yield areas reported for the trawling fleet operating for Argentine hake in northern Patagonia during the summer in the 1990s (Fig. 6; Crespo *et al.*, 1997). Argentine hake is a schooling, pelagic fish that moves inshore towards spawning grounds during late austral spring and summer, and that plays a pivotal role in the trophic ecology of the Patagonian shelf (Podestá, 1990; Ehrlich & de Ciechomski, 1992; Prenski & Angelescu, 1993). The highest concentration of hake larvae occurs during mid-summer months to the south-east of Península Valdés (Ehrlich & de Ciechomski, 1992) within the range of movements of the most pelagic females from Punta León and Punta Pirámide. Likewise, locations at sea of adult males coincide with expected high hake biomass concentration for that particular time of the year, and with historical movements of the Argentine fishing fleet (Perez-Comas, 1990; Podestá, 1990; Crespo *et al.*, 1997). In late November and early December, the period covered by the study of male sea lions, hake is migrating to the southern spawning area, south of Península Valdés (*c.* 42–47°S; Podestá, 1990). Evidence of an overlap with fisheries based on sea lion diet habits and fisheries operations exists for the South American sea lion population of the Falkland Island (Thompson *et al.*, 1998).

The reported broad-spectrum diet of South American sea lions (George-Nascimento, Bustamante & Oyarzun, 1985; Crespo *et al.*, 1997; Thompson *et al.*, 1998; Koen-Alonso *et al.*, 2000) may buffer the immediate effects of an overlap with fisheries. However, changes in the distribution and availability of preferred prey in relation to rookery location, may affect the foraging effort of a central place forager such as a lactating sea lion female (Boyd, McCafferty & Walker, 1997; Boyd *et al.*, 1998). A sub-optimal foraging condition for a mother attempting to optimize the return time to the pup will increase foraging costs and alter pup provisioning.

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