Diving behaviour of lactating southern sea lions (*Otaria flavescens*) in Patagonia

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Abstract: The diving behaviour of six lactating female southern sea lions (*Otaria flavescens*) was recorded during 52.4 animal-days at sea. Information was obtained from 18 057 dives. Females spent 52.7 ± 6.2% of the time at sea diving. Median and maximum dive depths ranged from 19 to 62 and from 97 to 175 m, respectively. Dives were short, with median and maximum durations ranging from 2.1 to 3.2 and from 4.4 to 7.7 min, respectively. Dives deeper than 10 m represented 56−89% of total dives and involved 93−97% of total diving time. Mean dive depth and duration of dives greater than 10 m were 61 m and 3 min, respectively. Most of these dives (69%) had a flat-bottomed U-shaped profile, bottom time constituting about half of the dive duration. Shallow dives, with a modal depth of 2 m, were short (median duration 0.1−0.8 min), with virtually no time spent at the bottom of the dive. During trips to sea, which ranged from less than 1 day to more than 4 days, females dove continuously. Mean dive frequency was between 11 and 19 per hour. Surface intervals were short (median 0.9−1.2 min) and there was no apparent diel variation in dive depth or frequency. The estimated aerobic dive limit of the females was exceeded on only a few dives (0.7−6.2%). Transit to potential foraging areas took 0.2−8.3 h.

Résumé : Le comportement de plongée a été étudié chez 6 femelles de l'Otarie australe *Otaria flavescens* par enregistrement de 52,4 animaux-jours en mer. Au total, 18 057 plongées ont été observées. Les femelles passaient en plongée 52,7% ± 6,2 de leur temps en mer. La profondeur médiane et la profondeur maximale de plongée allaient respectivement de 19 à 62 m et de 97 à 175 m. Les plongées étaient courtes, de durées médiane et maximale de 2,1−3,2 min et 4,4−7,7 min. Les plongées de profondeur supérieure à 10 m représentaient 56−89% de toutes les plongées et 93−97% du temps total passé en plongée. La profondeur moyenne des plongées de profondeur supérieure à 10 m était de 61 m et leur durée moyenne, de 3 min. La plupart de ces plongées (69%) affectaient le tracé d'un U à fond plat et le temps passé au fond du U était d'environ la moitié de toute la durée de la plongée. Les plongées peu profondes, à profondeur modale de 2 m, étaient courtes (durée médiane de 0,1−0,8 min) et les animaux ne passaient à peu près pas de temps au bas de la courbe de plongée. Au cours des excursions en mer, d'une durée de moins de 1 jour à plus de 4 jours, les femelles plongeaient continuellement. La fréquence moyenne des plongées était de 11 à 19 par heure. Les intervalles passés en surface étaient de courte durée (médiane 0,9−1,2 min) et la profondeur ou la fréquence des plongées ne semblaient pas varier en fonction de l'heure du jour. La limite estimée des plongées aérobiques des femelles n'a été dépassée qu'à quelques reprises (0,7−6,2%). La durée des déplacements vers des zones potentielles d'alimentation a été évaluée à 0,2−8,3 h.
[Traduit par la Rédaction]

Introduction

Most southern sea lions, *Otaria flavescens*, are distributed in the South Atlantic (King 1983), where some populations have never recovered from intense harvesting earlier this century (Reijnders et al. 1993). The world population is conservatively estimated to be 150 000 animals (Cappozzo and Rosas 1991; Reijnders et al. 1993).

In Patagonia, Argentina, about 500 000 animals were killed from 1918 to 1960 (Crespo 1988) and the population declined from an estimated 150 000 in the late 1940s (Carrara 1952) to 68 000 − 75 000 in 1990 (Szapkievich 1992). Some colonies, such as those in northern Patagonia, have remained stable during the last 25 years (Crespo and Pedraza 1991), but others have declined dramatically. Sea lions in the Falkland (Malvinas) Islands decreased from 380 000 animals in the late 1930s (Hamilton 1939) to 30 000 in the 1960s (Laws 1973; Strange 1979), 15 000 in the late 1980s (Reijnders et al. 1993), and 3000−4000 in the 1990s (D. Thompson, personal communication).

The reasons for the declines in southern sea lion populations are unknown. Since unusually high mortality rates have

not been evident on land, limiting factors are probably operating during the pelagic phase of their life cycle. Depletion of food resources has been cited, for example, as a potential cause of population declines in southern elephant seals, *Mirounga leonina* (Hindell 1990), harbour seals, *Phoca vitulina* (Loughlin 1991), harp seals, *Phoca groenlandica* (Blix 1991), and northern fur seals, *Callorhinus ursinus* (Loughlin 1991). Similarly, low food availability, including the potential effects of commercial fisheries, is a possible cause of the population decline in Steller sea lions (*Eumetopias jubatus*), the largest sea lions in the northern hemisphere (Loughlin 1991; Trites and Larkin 1992).

Availability and distribution of prey are reflected in the foraging patterns of sea lions and fur seals (family Otariidae) (Boyd and Croxall 1992; Gentry and Kooyman 1986; Costa 1991). Foraging strategies may be inferred, for example, from the depth, duration, shape, frequency, and diurnal distribution of dives (Croxall et al. 1985; Gentry and Kooyman 1986; Le Boeuf et al. 1988, 1989, 1993; Campagna et al. 1995). The pattern of diving is assumed to reflect the types of prey consumed (e.g., pelagic or benthic animals) (Costa 1991) and the effort expended to obtain it (Costa 1988). Interindividual variation in diving patterns may reflect different foraging strategies associated with different prey types.

Previous research on southern sea lions has emphasized social behaviour, breeding biology, and population dynamics (e.g., Hamilton 1934, 1939; Vaz-Ferreira 1975, 1981; Campagna 1985; Campagna and Le Boeuf 1988a, 1988b; Ximénez 1976; Lewis and Ximénez 1983; Crespo 1988; Crespo and Pedraza 1991). Here, we provide the first data on free-ranging behaviour for this species. Given that successful foraging immediately after parturition is vital for pup survival and population growth (Ono et al. 1987), we examined the at-sea behaviour of lactating females in coastal Patagonia.

We also attempted to obtain data on foraging sites in order to assess the potential temporal overlap with developing commercial fisheries. We also add *O. Flavescens*, a temperate-latitude species, to the growing comparative data base on foraging strategies in pinnipeds (e.g., Gentry and Kooyman 1986; Costa 1991).

Methods

The diving behaviour of six lactating southern sea lion females was studied using MK4 time−depth recorders (TDRs; Wildlife Computers, Woodinville, Washington) during the 1993 and 1994 breeding seasons (three animals each year) at Faro Punta Norte rookery, Península Valdés, Argentina (42°04'S, 63°47'W; see Campagna 1985). In this colony, the breeding cycle begins with the arrival of adult males during the first half of December, followed by the females. Most births occur between 10 and 25 January (Campagna 1985). Females copulate about a week after giving birth and go to sea to feed 2 days after mating. Thereafter, females alternate periods of feeding at sea (1−5 days) with periods on land nursing their pups (Campagna and Le Boeuf 1988a). Breeding ends by the second week of February.

Upon arrival at the colony, pregnant females were marked using multicoloured paint pellets (Campagna and Le Boeuf 1988a). Females were captured within a day after parturition,

using ropes and a hoop net (Flexi-Net, Fuhrman Diversified, La Porte, Texas). In 1993, females were weighed with a 500-kg (±2 kg precision of the scale) spring balance. In 1994, body size was visually estimated to minimize stress associated with handling. Females, ranging in mass from 100 to 165 kg, were anaesthetized with intramuscular injection of tiletamine hydrochloride with the sedative zolazepam hydrochloride (Telazol[R], Aveco Co., Inc., Fort Dodge, Iowa) at a dosage of 1.47−3.18 mg/kg (see also Boyd et al. 1990). In some cases, sedated females were then placed on a restraint board (Gentry and Holt 1982).

Following immobilization, the fur on the back of the animal was cleaned with acetone, and an adhesive (liquid neoprene) was worked into the hair. A TDR, glued to a neoprene patch and reinforced with plastic clamps, was then glued on the dorsal midline above the shoulders. The attachment was firm within 10 min. Instrumented animals were then tagged on the front flippers (Allflex tags) to facilitate identification upon recapture. Daily presence in the colony was recorded on identification cards for each marked female and her pup. In the 1994 breeding season, the three females studied in 1993 came back to the colony and pupped successfully, indicating no detrimental effects due to immobilization and TDR deployment the previous year.

Females went to sea within a week after instruments were attached. The TDRs were programmed to collect data as soon as females entered the water, recording hydrostatic pressure (dive depth) every 5−10 s.

TDRs were recovered 20−30 days after attachment, about 1 week before the end of the breeding season, just before the males abandoned their positions in the colony. Instrument recovery was facilitated by the presence of males, which prevented female stampedes. Recaptured animals were immobilized with Telazol (1993) or restrained in a net (1994) for instrument retrieval. The diving records provided time of day, depth, duration, and surface time of all dives performed by each female. Software supplied by Wildlife Computers (dive analysis and strip chart for MKII through MK5 time−depth recorders) provided summary analyses of the diving data. Dives of less than 2 m were excluded from analyses. The period from the start of the first foraging trip to the recovery of the TDR was "time with instrument."

Dives were divided into three components: descent, bottom (interval of constant depth), and ascent. Deep dives were categorized into one of three major types, using the time−depth profiles: flat-bottomed U-shaped dives had a direct descent to a sharp inflection point at the bottom of the dive that was followed by a flat horizontal period and then a direct ascent to the surface; irregular-bottomed U-shaped dives had a rapid descent, followed by a flat horizontal short period, a new descent to a final depth with no bottom time, and ascent to the surface (mirror images of this dive type were also present); V-shaped dives were sharply angled to the bottom of the dive, with no bottom time, followed by a nearly vertical ascent to the surface.

Transit time to potential foraging areas was the time interval between departure from the colony until an abrupt and persistent change to deep diving occurred (outward trip), or the time interval between the last series of deep dives until arrival at the colony (inward trip). Transit times were used as an estimate of the distance travelled before potential

Table 1. Summary of trips to sea for six female southern sea lions; data were obtained in 1993 and 1994 from time−depth recorders.

Female	No. of days with TDR	No. of foraging trips	No. of days recorded	Range of duration of foraging trips (h)	No. of dives/h
1993					
Vale	10	2	7.3	79−96	18.8
Madre	14	5	7.0	13−62	15.2
Circo	13	2	3.5	—	—
1994					
Rolfa	17	3	6.6	72−107	11.1
Errante	20	5	13.1	51−86	13.2
Flushy	21	4	15.0	95−101	15.2
Total	95	21	52.5		
Mean ± SD	15.8±4.3	3.5±1.4	8.8±4.4		14.7±2.9

Table 2. Summary statistics from the diving records of six female southern sea lions while at sea.

Female	No. of dives	Dive depth (m) Median	Dive depth (m) Max.	Dive duration (min) Median	Dive duration (min) Max.	Bottom time (min) Median	Bottom time (min) Max.	Surface interval Median (min)	Surface interval Max. (h)	No. of surface intervals >1 h	% time diving
Vale	3 277	34	99	2.1	5.7	0.7	3.7	0.9	2.8	5	56.4
Madre	2 557	19	112	2.3	7.3	0.8	5.7	1.1	1.4	3	53.3
Circo	858	55	97	2.5	4.4	1.3	3.3	—	—	—	—
Rolfa	1 750	47	175	2.8	6.5	0.8	3.8	1.2	5.4	8	45.0
Errante	4 159	62	110	3.2	7.7	1.7	5.8	1.2	2.0	7	60.6
Flushy	5 457	55	106	2.3	5.2	1.2	3.7	1.2	3.4	8	48.4
Total	18 058										
Mean ± SD		45±16	117±29	2.5±0.4	6.1±1.3	1.1±0.4	4.3±1.1	1.1±0.1	3.0±1.5	6±2	52.7±6.2

foraging behaviour began. To compare outward and inward transit times a paired Student's *t* test was used (Zar 1984). Aerobic dive limits (ADL) were estimated using Gentry and Kooyman's (1986) equation.

Results

We recorded 18 057 dives during 52.4 female-days at sea (Table 1). One female (*Circo*) went missing for 10 days during her second foraging trip. When she was resighted, she was abnormally thin and seriously wounded. Her TDR was damaged and part of the record was corrupted, preventing the analysis of some data. For the female *Rolfa*, we have only dive recordings from the first trip to sea, because the TDR failed during the second trip.

All females conducted 3−5 foraging trips during a period of about 3 weeks. Trip duration ranged from less than a day to more than 4 days (Table 1). The shortest trip lasted 13 h and occurred at night.

Females started diving soon after leaving the colony and dove almost continuously for the entire time at sea. The frequency of diving ranged from 11 to 19 dives per hour (Table 1). Transit to and from potential foraging areas took 0.2−8.3 h, outward and inward periods not being statistically different ($t = -0.31$, df = 14, $P < 0.05$). Based on

the surface swimming speed of a Hooker's sea lion (*Phocarctos hookeri*), which is similar in size to a southern sea lion (1.2 m/s; Ponganis et al. 1990), and assuming that the animals swam in a straight line, the minimum distance travelled to and from potential feeding areas was 0.9 km.

Females spent approximately half of their time at sea diving (Table 2). Median dive duration ranged from 2 to 3 min (Table 2). Most dives (91%) were shorter than 4 min (Fig. 1); the longest lasted 7.7 min. Most dive durations (94−99%) were within the ADLs of the females (Table 3).

The median dive depth ranged from 19 to 62 m, with one female exhibiting maximum dives exceeding 170 m (Table 2); 93% of all dives were less than 80 m deep (Fig. 2).

The frequency distribution of maximum dive depths was bimodal. Dives were therefore grouped for further analyses into shallow (< 10 m) and deep (≥ 10 m) dives. Dives ≥ 10 m represented 56−89% of all dives. These dives involved 93−97% of the total diving time. Dives that exceeded 10 m had a mean depth of 61 m and lasted about 3 min (Table 4). About half of the duration of these dives was spent at the bottom of the dive (Table 4). Shallow dives (2.1−10 m; $N = 5845$) were short (median duration 0.1−0.8 min) and occurred at a modal depth of 2 m, with virtually no time spent at the bottom of the dive.

Generally, the females exhibited a dive pattern consisting

Fig. 1. Frequency distribution of dive durations for six southern sea lion females combined (N = 18 058).
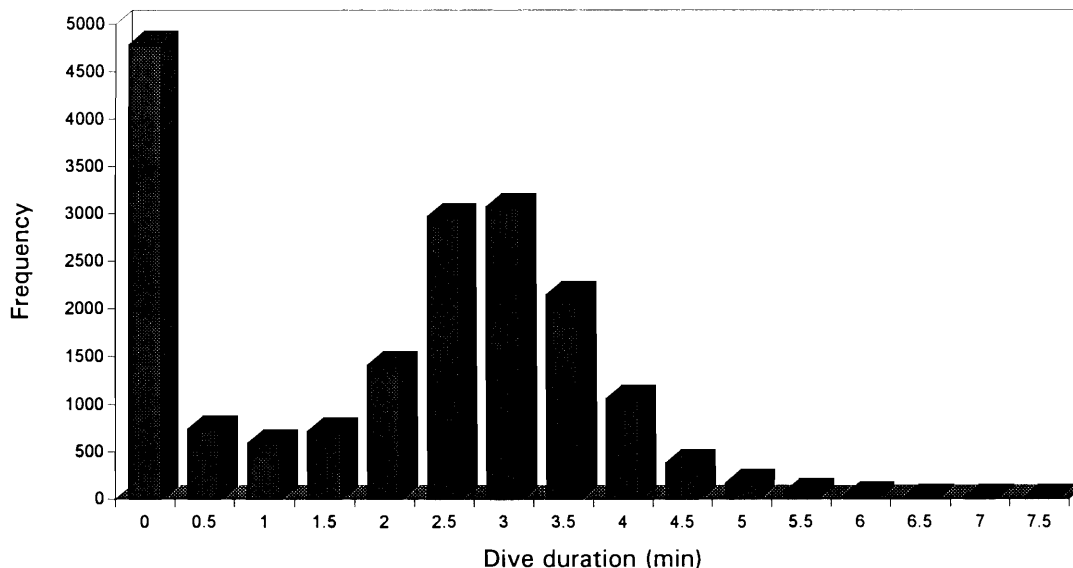
Fig. 2. Frequency distribution of dive depths for six southern sea lion females combined (N = 18 058).
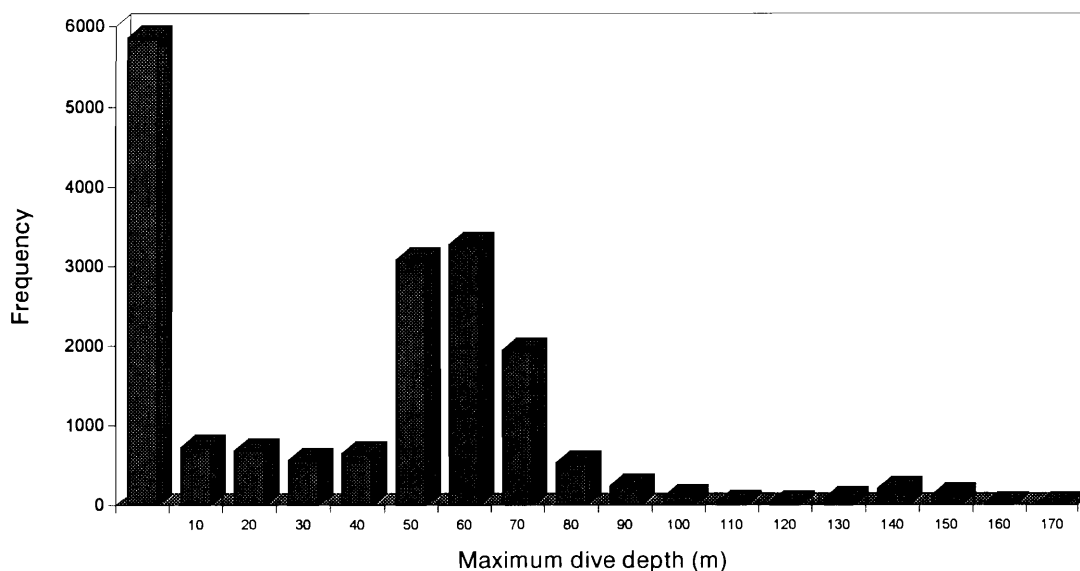
Table 3. Female body size, estimated aerobic dive limit (ADL), and percentage of dives exceeding ADL for six female southern sea lions.

Female	Mass (kg)	Estimated ADL (min)	% dives > ADL
Vale	131	4.5	0.7
Madre	165	4.7	7.1
Circo	121	4.5	0.0
Rolfa	120[a]	4.5	5.9
Errante	120[a]	4.5	6.2
Flushy	100[a]	4.3	1.1

[a]Female body size was visually estimated in 1994.

of a long series of flat-bottomed U-shaped dives. This dive type constituted around 69% of all deep dives (Table 5). Almost all of the remaining profiles for deep dives were irregular-bottomed U-shaped dives.

The median surface interval between dives ranged from 0.9 to 1.2 min. Females had 3−8 surface intervals longer than 1 h during foraging trips, the duration ranging from 1.4 to 5.4 h (Table 2). One female dove continuously for 44 h (526 dives) without a surface interval longer than 14 min.

Dive depth and frequency did not show an apparent diel pattern in most females (Fig. 3). One female dove deeper during daylight hours (Fig. 4).

Discussion

The general diving pattern of lactating female southern sea lions in Patagonia consists of series of relatively shallow, short,

Fig. 3. Dive depth versus time of day for all dives of female *Vale*. As for most females, no diel pattern is evident.
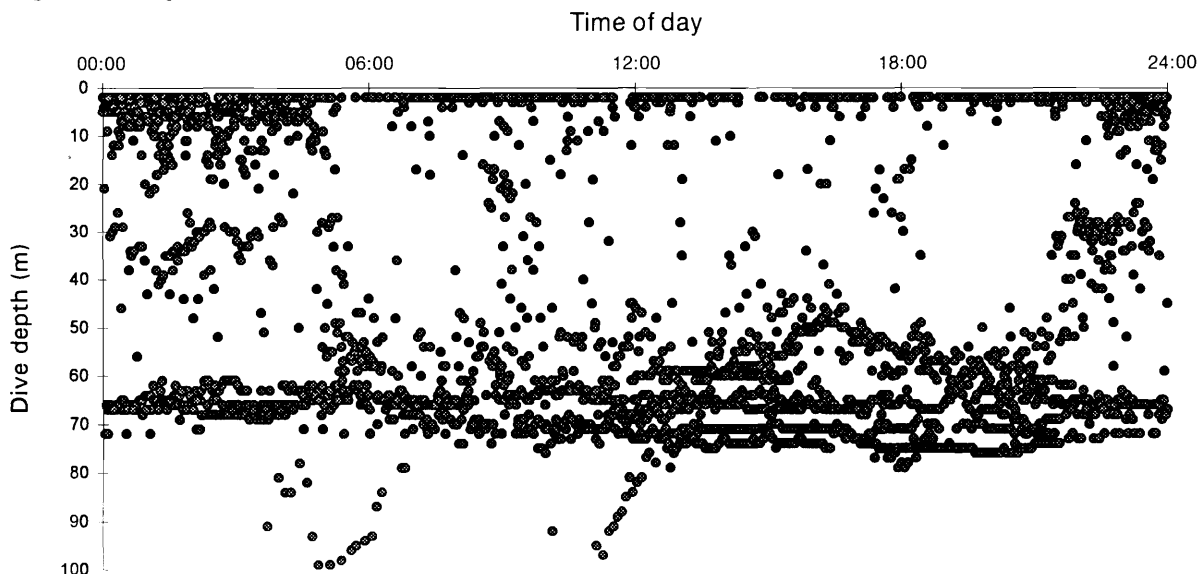
Table 4. Summary diving statistics for dives ≥ 10 m for six southern sea lion females.

Female	No. of dives	Dive depth (m) Mean	Dive depth (m) Max.	Dive duration (min) Mean	Dive duration (min) Max.	Bottom time (min) Mean	Bottom time (min) Max.
Vale	1 898	57.8±16.9	99	2.9±0.7	5.7	1.5±0.7	3.7
Madre	1 430	54.7±22.4	112	3.5±1.0	7.3	1.9±0.9	5.7
Circo	761	56.3±21.8	97	2.5±0.7	4.4	1.4±0.6	3.3
Rolfa	1 217	88.4±49.9	175	3.3±0.9	6.5	1.3±0.6	3.8
Errante	3 220	64.2±16.4	110	3.5±0.8	7.7	2.0±0.8	5.8
Flushy	3 687	53.9±14.4	106	2.7±0.6	5.2	1.5±0.6	3.7
Total	12 213						
Mean		60.9		3.1		1.7	
Mean ± SD			117±29		6.1±1.3		4.3±1.1

Table 5. Percent distribution of deep dives (≥ 10 m) for six female southern sea lions in relation to dive-profile types.

| Female	Dive type Flat-bottomed U-shaped	Dive type Irregular-bottomed U-shaped	Dive type V-shaped
Vale	61.4	37.0	1.6
Madre	77.6	21.5	0.9
Circo	72.3	26.4	1.3
Rolfa	45.7	52.8	1.5
Errante	83.1	16.6	0.4
Flushy	76.2	23.3	0.5
Mean ± SD	69.4±13.7	29.6±13.2	1.0±0.5

flat-bottomed dives with no apparent diel variation in depth or frequency. Flat-bottomed dives start shortly after females leave the rookery and continue until they return to shore. Females spend a large proportion of time at the bottom of most dives.

The dive pattern suggests that females are foraging either near the bottom or at a preferred depth. All females, however, showed a proportion of mesopelagic dives, with vertical excursions (Figs. 3 and 4), suggesting that they may also chase prey in the water column. In addition, transit times suggest that foraging areas are close to the breeding rookery.

Diet composition studies, based on analyses of scats and the stomach contents of dead animals, support the conclusion that female southern sea lions are coastal foragers which concentrate their effort on benthic prey (Koen Alonso 1993). The most common items found in their diet are bottom-dwelling fishes and octopods found in shallow, coastal waters. Interindividual variation in diet composition is high. Female southern sea lions eat at least 13 species of fish, 5 species of squid and octopods, and 3 species of crustaceans.

The overall dive pattern of southern sea lions is similar to that of other sea lion species. Hooker's sea lions, for example, are also bottom feeders that dive repetitively, searching for octopods on rocky bottoms or preying on squid during 90−120 m deep dives that last 4−5 min. Like southern sea lions, they do not exhibit a diel diving pattern. Depth attained

Fig. 4. Dive depth versus time of day for all dives of female *Rolfa*. This female dove deeper during daylight hours (06:00−21:00).
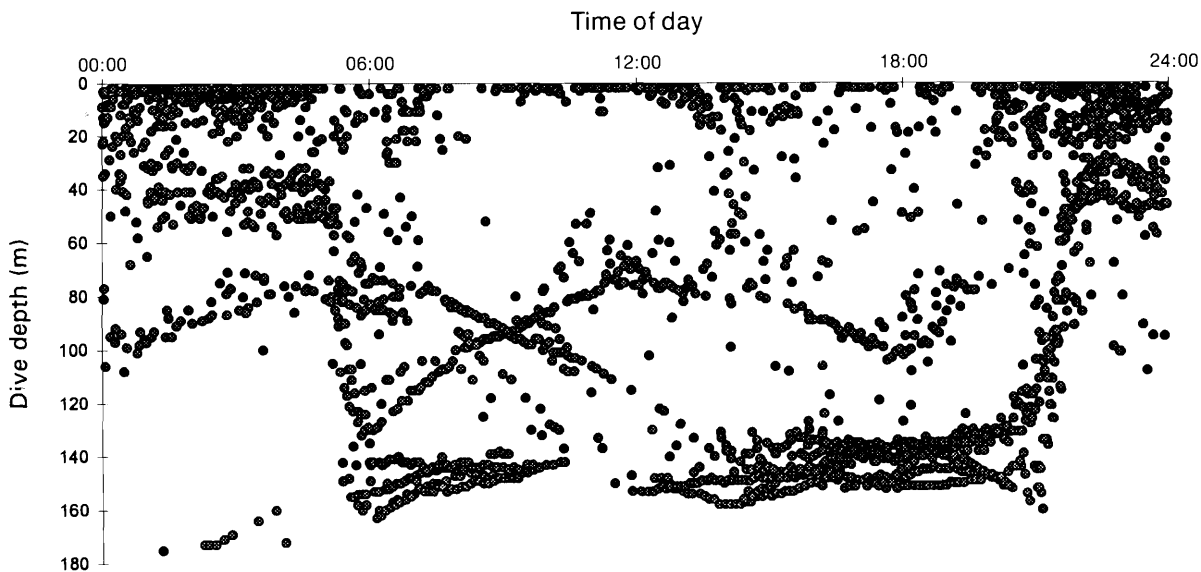
by Hooker's sea lion females is apparently limited by the underwater topography of the Auckland seamount, where most feeding occurs (R. Gentry, personal communication). Similarly, female Australian sea lions, *Neophoca cinerea*, are shallow divers that begin foraging soon after leaving the rookery. The diving profile follows the bottom contour until preferred depths are reached (Costa et al. 1989a). Steller sea lions also forage close to land during the breeding season, making brief trips and diving to shallow depths (<30 m) (Merrick and Loughlin 1993).

In other species, like the Galapagos sea lion (*Zalophus californianus wollebaeki*), dives are also short and shallow, and foraging areas are close to the rookery. However, in this species, more than 50% of all dives occur during daylight hours (Kooyman and Trillmich 1986). California sea lions, *Zalophus californianus*, also perform shallow, short dives, the majority being less than 3 min in duration and 80 m in depth (Feldkamp et al. 1989). During the spring and summer breeding season, these sea lions feed mainly on schooling, vertically migrating species of fish and squid (Antonelis et al. 1984). Thus, they display diel variations in dive depth that seem to be a response to the diel distribution of their prey.

In contrast, some fur seals have a diving−foraging behaviour that differs in several important aspects from that of the southern sea lion, and sea lions generally. Fur seals are short-duration, shallow divers that have a tendency to dive at night. Generally, nighttime dives tend to be shallower than daytime dives, apparently reflecting the vertical movement of prey species. Furthermore, diving in these species is organized into bouts and, in general, the animals do not spend measurable amounts of time at the greatest depth attained (e.g., Croxall et al. 1985; Kooyman and Gentry 1986; Gentry et al. 1986; Kooyman and Trillmich 1986; Kooyman et al. 1986; Boyd and Croxall 1992).

Despite the differences between sea lions and fur seals, the dive frequency (number/h) in southern sea lions corresponds to the dive frequency within bouts for northern fur seals. *C. ursinus* (Gentry et al. 1986), Antarctic fur seals,

Arctocephalus gazella (Kooyman et al. 1986), South African fur seals, *Arctocephalus pusillus* (Kooyman and Gentry 1986), and Galapagos fur seals, *Arctocephalus galapagoensis* (Kooyman and Trillmich 1986).

Interspecifically, larger otariids tend to dive deeper than small ones (Costa 1991). Being among the largest of the sea lions, *O. flavescens* would be expected to be a deep diver. Hooker's sea lion, which is similar in size to southern sea lions, has been recorded to dive to 460 m (12 min dive duration) (Gentry et al. 1987). In our study, the rather shallow maximum depths for *O. flavescens* presumably reflect the shallow, broad continental shelf off the coast of Patagonia (Campagna et al. 1995) rather than a limiting physiological factor in diving capability.

In terms of energy expenditure and energy intake, an efficient foraging strategy for lactating females that leave their pups alone ashore is to spend short trips foraging in areas close to shore, where food is readily available. Females are thus expected to (*i*) decrease transit time to and from foraging areas; (*ii*) maximize time spent diving by performing dives within the ADL, with reduced surface time (rather than long dives followed by inactive periods at the surface); (*iii*) dive continuously; and (*iv*) dive to shallow depths, minimizing the ascent−descent component of the dive and maximizing time at the bottom of the dive. Our females, and those of most sea lion species during the breeding season, closely follow the expected, energy-maximizing diving−foraging pattern (Gentry et al. 1987; Costa et al. 1989a; Feldkamp et al. 1989; Merrick and Loughlin 1993).

The southern sea lion shares the shores of Península Valdés with a growing population of southern elephant seals (Campagna and Lewis 1992). However, the specialized deep-diving foraging strategy of elephant seals suggests little overlap in foraging areas and, therefore, little potential for competition for food with sympatric sea lions (Campagna et al. 1995).

Foraging in most marine mammals and seabirds, as well as human fishing activities, take place at depths where sea lions and fur seals feed (Kooyman and Gentry 1986; Costa

1991). Sea lions in Patagonia forage in an area of expanding commercial fisheries (Csirke 1987; Anonymous 1994). Indeed, the offshore southwest Atlantic fishery has become one of the fastest growing commercial fisheries in the world, landing 800 000 t in 1985, compared with 100 000 t in 1970 (Csirke 1987). Likewise, coastal fisheries in Argentina, which produced more than 900 000 t of fish and cephalopods in 1993 (Anonymous 1994), operate within a few kilometres of major sea lion colonies.

Fisheries have the potential to have a strong impact on marine mammal food availability by reducing preferred prey items (e.g., Blix 1991). Reduced prey availability affects pinniped populations by lowering rates of milk intake by pups, by reducing growth rates of pups and juveniles, or through increasing mortality (Ono et al. 1987; Costa et al. 1989b). Under conditions of reduced food availability, increased foraging effort and energy expenditure would be expected (Costa et al. 1989b).

Although there is no evidence that fisheries in the South Atlantic are currently affecting sea lion populations, fisheries have been implicated in the decline of other pinnipeds, such as the Steller sea lion (Trites and Larkin 1992).

The data presented in the present paper, therefore, provide base-line data for monitoring potential interactions between sea lions and developing commercial fisheries in Patagonia. Further research on the diving behaviour of this species, especially studies using satellite transmitters to determine specific foraging areas visited by southern sea lions and their potential overlap with fisheries, would complement the present observations.

Acknowledgements

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