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## On- and off-shelf diving effort of juvenile elephant seals from Península Valdés determined by light loggers

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The shallow Patagonian Shelf off Península Valdés limits the dive depth of southern elephant seals (*Mirounga leonina*) to <100 m, an unusual circumstance for this deep-diving species. Beyond the shelf water depths of >1,000 m enable the seals to forage deeper and use the entire water column. We compared the diving pattern of 10 juveniles instrumented with light–temperature loggers to determine if diving effort, measured as dive durations longer than the estimated aerobic dive limit, differed between on-shelf and off-shelf waters. The productive Patagonian Shelf, an environment where juveniles showed lower diving effort, also was used commonly by older seals, which likely displaced juveniles off-shelf periodically, where they exhibited increased diving effort.

Key words: diving effort, light–temperature loggers, *Mirounga leonina*, Patagonian Shelf

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Foraging ability (the capacity of a seal to locate, capture, and ingest food) is a function of diving ability (Irvine et al. 2000; Kooyman et al. 1983). Being smaller, and sometimes with less-developed oxygen storage capacity, juveniles have lower dive capabilities than adults (Irvine et al. 2000). Their diving ability improves with age, gradually increasing in both depth and duration (Hassrick et al. 2007; Irvine et al. 2000; Le Boeuf et al. 1996; Thornton et al. 2005; Zeno et al. 2008). Dive durations ultimately are determined by stored oxygen reserves, and the aerobic dive limit (calculated as the estimated usable oxygen stores divided by the estimated rate of oxygen consumption during diving) defines the theoretical upper limit to dive duration for aerobic dives. Dives exceeding the aerobic dive limit define increased diving effort and require anaerobic metabolism with the consequent detrimental effects associated with increased plasma lactate (Williams 2001). Relative indicators of increased diving effort include increased proportion or durations, or both, of extended dives and extended surface intervals (Irvine et al. 2000). Such increased diving effort leads to a series of short dives after an extended dive (Kooyman et al. 1980, 1983), which is required to clear the lactic acid accumulated during long anaerobic dives (Costa et al. 2001). Increases in diving effort can compromise foraging ability, foraging success, and ultimately survival rates (Irvine et al. 2000). Foraging location also affects diving behavior (Irvine et al. 2000) of elephant seals on the continental margins, where dives are

bathymetrically constrained to be short and shallow (Campagna et al. 1998, 1999; Le Boeuf et al. 1996, 2000a, 2000b; McConnell et al. 1992; Webb et al. 1998), which may lead to reduced diving effort compared to foraging in the deep open ocean.

The continental elephant seal colony on Península Valdés in Patagonia, Argentina, is adjacent to one of the largest (almost  $1 \times 10^6$  km<sup>2</sup>), shallowest (mostly <150 m deep), and most productive shelves in the world (Bisbal 1995). The shelf supports a variety of top predators (Acha et al. 2004; Croxall and Wood 2002). The Patagonian Shelf extends to 850 km before reaching deep open ocean (Acha et al. 2004). Most other elephant seal colonies inhabit relatively narrow shelves < 100 km wide that deepen abruptly to >1,000 m (Campagna et al. 2007). Although adults are breeding (September–November) or molting (January–March) on Península Valdés, juveniles are at sea foraging (Lewis et al. 2004). Juveniles (1–4 years old) molt in November and also are recorded in low numbers from March until July (Lewis et al. 2004). Some juveniles remain in shallow shelf waters, diving uniformly to depths of 100–115 m for periods of 12–18 min per dive (Campagna et al. 2007). Others migrate to distant oceanic areas, where dives can be up to 5 times deeper (Campagna et al. 2006).



This study compares the dive patterns of juvenile southern elephant seals (*Mirounga leonina*) from Patagonia to determine if the diving effort (extended dives and long surface intervals) differs on and off the shelf. We propose that deeper off-shelf waters require deeper and longer dives, resulting in a diving effort that may impact juvenile foraging success and survival. Specifically, we hypothesized that deep-diving juveniles exert greater diving effort than do shallow divers, and that this will be reflected in the duration and proportion of long dives and the duration of surface intervals following long dives. To test this hypothesis, we deployed relatively affordable light-temperature loggers (LTLs).

## MATERIALS AND METHODS

Ten juveniles (2–3 years old; 5 males and 5 females), equipped with satellite tags (SPOT4/SPOT5; Wildlife Computers, Redmond, Washington) during postresting and postmolting trips between 2005 and 2006, were instrumented simultaneously with LTLs (Platypus Engineering, Sydney, Australia). Both devices were attached to juveniles on Península Valdés, Patagonia, Argentina (42°45'S, 63°38'W), following protocols detailed in Campagna et al. (2006, 2007), and complete tracks of 7 of these animals are described here.

The approximate age of juveniles was estimated from body shape, length, girth, and secondary sexual characteristics (Campagna et al. 2007). Standard length (SL) and girth (G) of juveniles in ventral recumbency were measured during deployment of instruments at haul-out sites to estimate body mass at departure, following Bell et al. (1997—body mass = 53.896 SL<sup>1.063</sup> G<sup>1.697</sup>). Procedures in this study complied with current laws of Argentina and with the guidelines for mammal research established by the American Society of Mammalogists (Gannon et al. 2007).

*Estimation of dive parameters.*—The LTLs are designed to measure light and temperature of the water column every sampling interval time during dives. Recorded data are used to estimate foraging locations. Each record of light and temperature has an associated date and hour expressed as hh/mm/ss. In this study sampling interval time was set at 30-s intervals, and light-time records were applied to estimate dive parameters, because movements up and down the water column are immediately reflected by changes in light level. Dive durations and surface intervals were estimated by simulations of dives at sea, using a cage with LTLs fixed inside. This allowed estimation of the minimum light level at the sea surface. Dive simulations were made from a boat and from a wharf for 20 min each at depths <35 m during different weather conditions (total or partial or no cloud cover at 1200 h in all situations) to account for variations of light availability at sea surface. Dive simulations also were made considering different orientations of the light sensor (at 90°, 180°, and 270° with the surface), because seals move in a 3-dimensional space. Elephant seals also can roll over and sink on their backs adopting a belly-up posture during the descent phase of drift dives, although such behavior does not start until seals reach a

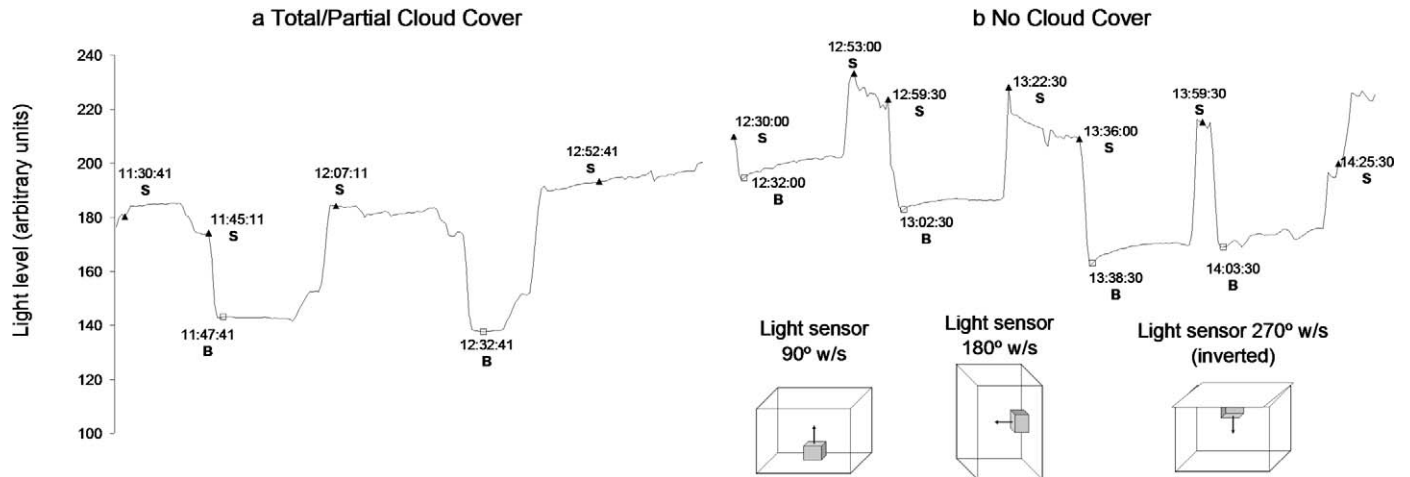
depth of  $\geq 135$  m (Mitani et al. 2009). Light saturation levels at the surface during total or partial cloud cover condition were 15% lower than when the sky was clear, and orientations of 180° and 270° of the light sensors in relation to the surface reduced the highest saturated light levels (at 90°) by 1% and 5%, respectively (Fig. 1). Based on these results and the range of light-level values recorded by LTLs throughout all months of the year, between 2 (total darkness) and 250 (light saturation) arbitrary units, we considered a conservative minimum value of saturated light level of 190 units. Records from the water column with levels >190 units were considered to be sea-surface values. Dive durations and surface intervals of juveniles were estimated based on this criterion, considering diurnal records between 0600 and 1700 h of the LTLs (local time; Fig. 2). Data recorded during night and long dives during hours of attenuated daylight (sunrise and sunset) in the winter months (when duration of daylight is shorter and light availability along the water column is lower) were not included in the analysis.

*Diving in 2 contrasting areas.*—Dive records were associated with satellite locations (based on date and local hh/mm/ss) to classify dives as on-shelf (On-S) or off-shelf (Off-S). Satellite locations of estimated accuracy of <150 m (class 3), 150–350 m (class 2), 351–1,000 m (class 1), >1,000 m (class 0), and those with no estimate of their accuracy (classes A and B) were used. An iterative forward-backward averaging filter was applied to reject records that would require an unrealistic travel rate >2.8 m/s (10 km/h—Campagna et al. 2007). Positions of dive records between satellite locations were estimated by linear interpolation, resampling sites at 1-h intervals. Extended dives were those exceeding the mean calculated aerobic dive limit estimated for juveniles from Península Valdés (15.87 min). The calculated aerobic dive limit value estimate is based on equations in Kooyman (1989), considering estimated total body stores of oxygen in lean mass ( $\bar{X} = 77$  kg) and a resting metabolic rate (oxygen consumption rate) of 0.0113 kg<sup>0.75</sup> (M. N. Lewis, pers. obs.). Extended surface intervals were those >5 min (Campagna et al. 1998).

*Statistical analysis.*—Pearson correlations were used to test for relationships between the body mass at departure and dive duration (Zar 1984). Diving effort, in terms of the number of extended dives and long surface intervals after long dives, was compared between On-S and Off-S areas using Student's *t*-tests (Zar 1984). Normal probability plots of the residuals and Levene's test were used to evaluate if data met the assumptions of normality and homoscedasticity, respectively. Statistical analyses were conducted using STATISTICA software (StatSoft, Tulsa, Oklahoma), with levels of significance set at  $P < 0.05$ . Means are reported with *SDs*, unless noted otherwise.

## RESULTS

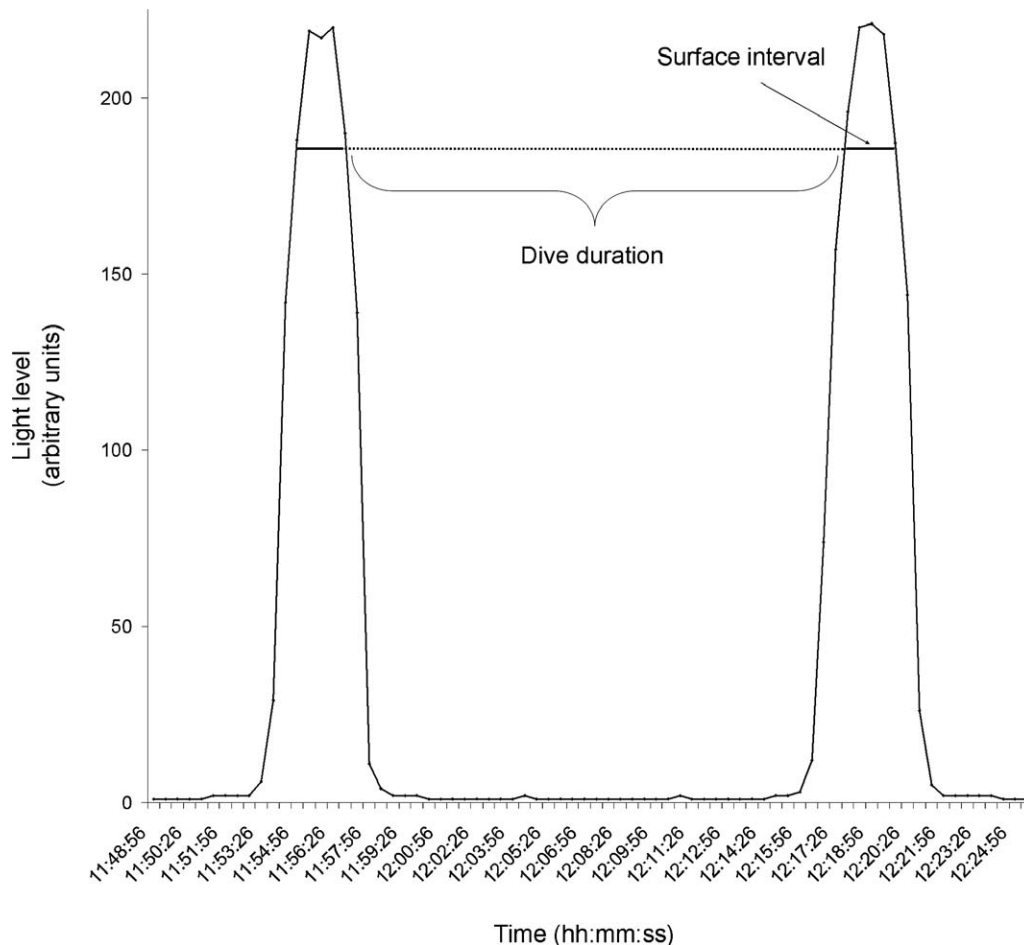
A total of 43,286 dives were estimated from light records of 10 LTLs recovered. Approximately half of these dives ( $n = 20,793$ ) were matched with satellite-based locations. Of those,



**FIG. 1.**—Dive simulations during: a) total or partial cloud cover in July (winter) and b) no cloud cover in September (spring), using 3 different orientations with the surface (w/s; 90°, 180°, and inverted). Light-level values presented are mean values from  $n = 9$  light-temperature loggers (LTLs). S = surface, B = bottom.

70.3% occurred On-S. Three juveniles remained exclusively On-S; the remaining 4 visited both habitats (Fig. 3a). Estimated body mass of juveniles at departure ranged from 125 to 197 kg. We found no relationship between body mass at departure and dive duration for either On-S and Off-S dives ( $r = 0.05$ ,  $n = 17$ ,  $P = 0.83$ ).

Based on dives matched with satellite-based locations ( $n = 20,793$ ), all seals exhibited extended dives longer than the calculated aerobic dive limit (17.1–23.1 min; Table 1; Fig. 3). A significantly lower proportion of extended dives occurred On-S ( $4.9\% \pm 5.1\%$  versus  $47.1\% \pm 25.8\%$  Off-S;  $t_{15} = -5.09$ ,  $P < 0.001$ ; Table 1). The average duration of the



**FIG. 2.**—Estimation of diving parameters based on light measurements of the water column (extract from a dive profile).

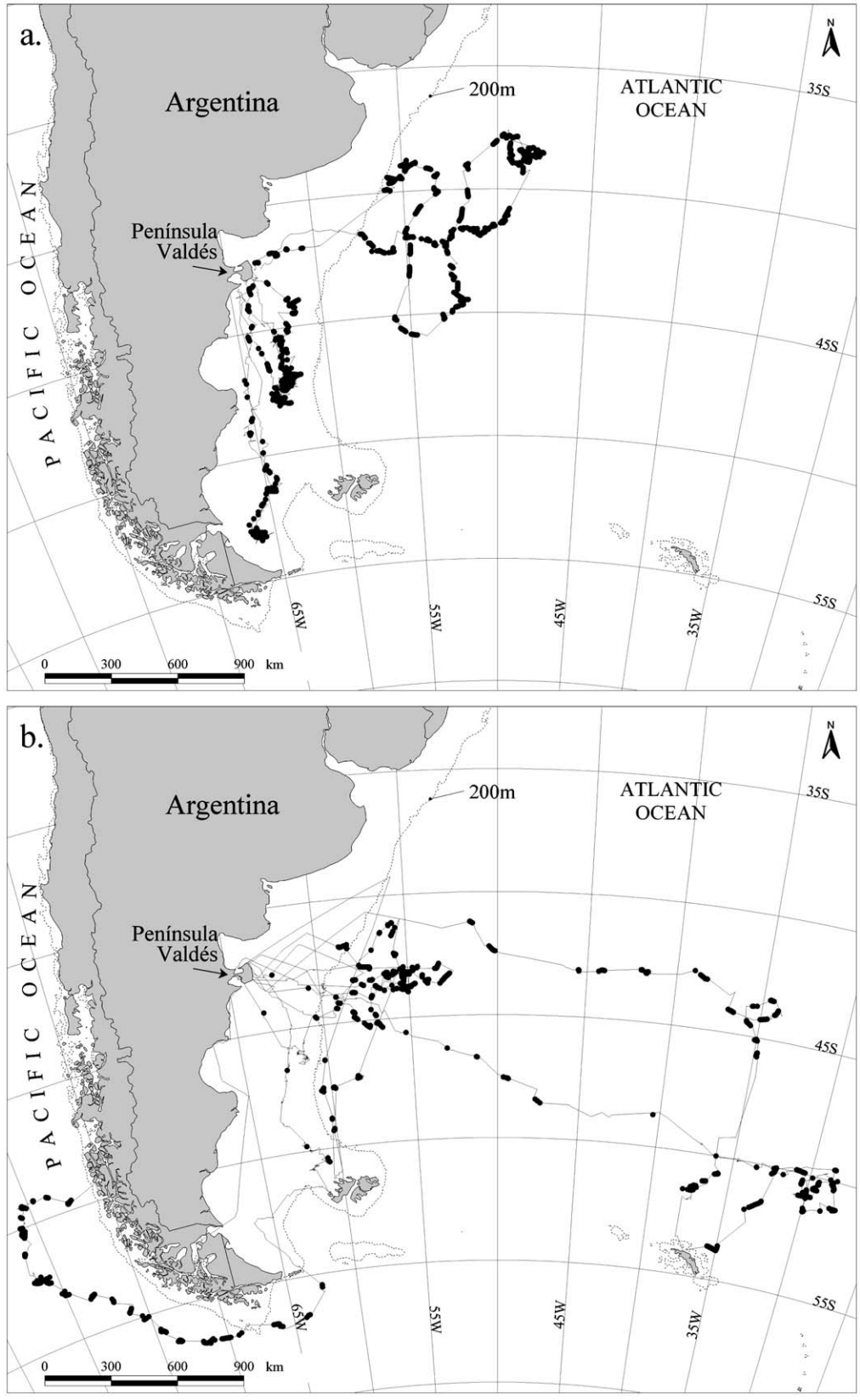


FIG. 3.—Travel trajectories of juveniles tracked during a) postresting trip in 2005 ( $n = 4$ ) and b) postmolting trip in 2005–2006 ( $n = 6$ ). Dive records with durations longer than the calculated aerobic dive limit are indicated with dots. The 200-m isobath is shown indicating the limits of the Patagonian Shelf.

**TABLE 1.**—Diving parameters for on-shelf (On-S) and off-shelf (Off-S) dives estimated by light levels (mean  $\pm$  SD).  $n$  = number of dives, ED = extended dive, ESI = extended surface interval.

Individual	Sex	$n$	% of ED	Duration of ED (min)	% ESI (>5 min)	Duration of ESI (min)
<b>On-S</b>						
LIN3	Female	218	0	—	1.8	7.3 $\pm$ 3.6
SUR1	Female	226	5.3	17.2 $\pm$ 1.4	0	—
MAR3	Female	471	8.7	18.8 $\pm$ 4.1	9.1	19.1 $\pm$ 18.7
FAR11	Female	3,234	0.6	17.1 $\pm$ 1.4	0.4	20.5 $\pm$ 18.6
RUS2	Female	197	1.0	18.0 $\pm$ 2.1	10.2	8.6 $\pm$ 4.6
RON6	Male	1,057	1.7	18.7 $\pm$ 5.2	1.6	24.6 $\pm$ 32.0
S14	Male	3,071	12.5	17.7 $\pm$ 2.1	1.3	22.4 $\pm$ 28.3
PT7	Male	172	0	—	4.1	14.6 $\pm$ 10.0
SyS2	Male	3,059	6.4	17.9 $\pm$ 1.9	0	—
BK6	Male	2,913	12.9	18.0 $\pm$ 4.0	2.1	37.2 $\pm$ 60.4
$\bar{X}$			4.9 $\pm$ 5.1	17.9 $\pm$ 0.6	3.1 $\pm$ 3.7	19.2 $\pm$ 8.9
<b>Off-S</b>						
LIN3	Female	2,165	32.5	22.8 $\pm$ 6.5	1.4	9.8 $\pm$ 12.0
SUR1	Female	764	47.0	19.0 $\pm$ 3.5	2.4	18.6 $\pm$ 23.9
MAR3	Female	1,809	91.8	23.1 $\pm$ 3.8	1.7	55.8 $\pm$ 91.9
FAR11	Female	984	47.1	18.6 $\pm$ 2.9	1.9	7.9 $\pm$ 2.7
RUS2	Female	453	57.6	21.2 $\pm$ 4.3	1.4	6.3 $\pm$ 1.2
RON6	Male	128	6.3	20.2 $\pm$ 10.6	5.5	8.7 $\pm$ 2.7
PT7	Male	256	47.3	19.0 $\pm$ 2.5	0	—
$\bar{X}$			47.1 $\pm$ 25.8	20.6 $\pm$ 1.9	2.0 $\pm$ 1.7	17.9 $\pm$ 19.1

extended dives also was shorter On-S than Off-S (17.9  $\pm$  0.6 min versus 20.6  $\pm$  1.9 min, respectively;  $t_{15} = -2.21$ ,  $P < 0.05$ ; Table 1). Extended surface intervals followed <0.5% of extended dives ( $n = 4,628$ ). In general, extended surface intervals were rare (0–10.2%; Table 1), with a mean duration of 18.7  $\pm$  13.7 min (7.3–55.8 min). All seals that foraged in both areas increased the number and duration of long dives when they moved to Off-S waters. Not all seals showed this same pattern in the numbers and durations of long surface intervals (Table 1).

## DISCUSSION

Our results were based on an indirect method for determining dive parameters. LTLs as dive recorders offer a less-expensive alternative (in the order of hundreds of US\$) to time–depth recorders and more-accurate satellite-relayed dive profiles (Myers et al. 2006—cost per tag approximately US\$1,200 and \$2,400, respectively). These simple, small, and low-cost devices are appropriate for pilot and low-budget studies whenever animals can be recaptured and instruments retrieved. Because of the lower cost they offer the potential of larger sample sizes. Although we do not have direct validation for the tags, the mean dive durations and mean surface intervals obtained from a time–depth recorder (samples taken every 5 s) and those calculated from an LTL, deployed simultaneously on juvenile male BK6, were similar: 12  $\pm$  3 and 1.5  $\pm$  0.3 min (Campagna et al. 2007) versus 12.6  $\pm$  3.3 and 2.2  $\pm$  0.6 min, respectively. Further, the values of mean dive duration of 11.8  $\pm$  4.6 min and mean surface intervals (< 5 min) of 2.0  $\pm$  0.3 min, estimated here from light levels, are in the range of mean dive durations and mean surface intervals reported for juveniles elsewhere, based on time–depth recorders (1–4 years old, 10.9–20.3 min and 1.4–

2.8 min, respectively—Andrews et al. 1997; Campagna et al. 2007; Le Boeuf et al. 1996; Webb et al. 1998). Although accuracy of geolocating by light levels was found to be low around the vernal and autumnal equinoxes (De Long et al. 1992), more recent methods are not affected as much by equinoxes (Sumner et al. 2009). The low cost and larger sample of studied animals provided by the use of LTLs confer some advantages over satellite telemetry to track movements at sea (Fuller et al. 2008). In the same way, variations of light intensity through the water column can provide a less-expensive and more statistically powerful approach to quantifying dive behavior. LTLs have other possible uses, because variation of temperature in the water column at local scales could be associated with the distribution of potential prey (when this information becomes available). Furthermore, variation of light intensity in the water column or light attenuation possibly could be linked to concentrations of phytoplankton assemblages as an index of primary productivity (Behrenfeld and Boss 2003), although this would require more experimental work.

Diving effort of juveniles foraging on the shallower Patagonian Shelf was less than in Off-S waters. Although juveniles are as capable as adults of long-distance travel, they are not as capable of long or deep dives (Campagna et al. 2007; Field et al. 2005; Hindell et al. 1999; McConnell et al. 2002). However, when foraging off the Patagonian Shelf, the seals typically made long and deep dives. Mean dive duration and proportion of extended dives was not related to mass, suggesting that the seals were not restricted physiologically to be submerged for short periods and consequently were not constrained to forage over the shelf. Elephant seals usually do not display anaerobic diving behavior, as evidenced by extended surface intervals or bouts of short dives following an extended dive; they rarely exceed their aerobic dive limit

(Hindell et al. 1992; Irvine et al. 2000; Le Boeuf et al. 1989; Slip 1997). Similarly, in the present study extended surface intervals were rare in both On-S and Off-S areas. Short dives after extended dives (those that averaged less than the mean duration of dives between consecutive extended dives) were detected in only 4 animals and in low numbers (up to 5 times) in relation to their total extended dives (up to 1,661). As has been suggested in other studies, it is possible that the theoretical aerobic dive limit equation underestimates the true aerobic capacity of these juveniles, and seals might be capable of making behavioral or physiological metabolic adjustments to increase their aerobic dive limit and solve their functional demands (Hassrick et al. 2007; Irvine et al. 2000; Le Boeuf et al. 2000b; Slip 1997; Thompson and Fedak 1993).

Nevertheless, juveniles foraging in oceanic habitats had a higher diving effort than those on the shelf. Reasons why juveniles choose to forage in more distant areas versus a closer foraging area where resources are apparently more readily available are still unknown. However, intraspecific competition might play a role. The recent satellite tracks of 6 juveniles (C. Campagna, pers. obs.) and 7 other juveniles described in Campagna et al. (2006, 2007) indicated that 75% of the seals foraged over midshelf and shelf-break areas, and the remaining 25% dispersed in the open ocean, during the time when adult seals are breeding on the coast (from August to November). In contrast, during the months when most of the population (juveniles and adults) are at sea (January–August), only 2 (18%) of 11 juveniles foraged On-S. Six of the remaining 82% were dispersed widely over oceanic areas, and 3 of them used the shelf or the shelf break only partially or in transit to off-S waters. Moreover, 11 subadult males at sea during these months (5–6 years old—C. Campagna, pers. obs.) were concentrated predominantly on the highly productive shelf and shelf-break areas, possibly as a consequence of their higher energetic demands directly related to larger body sizes. The Patagonian Shelf is therefore intensively used by different age classes of the elephant seal population, which likely produces intraspecific competition or resource partitioning by means of age–class segregation.

Yearlings from Macquarie Island, because of their smaller body size and relative oxygen stores, make shorter dives than do larger juveniles (Hindell et al. 1999; Irvine et al. 2000). Yearlings in Patagonia therefore would be expected to forage inside the limits of the Patagonian Shelf if they could do this more profitably than foraging Off-S. However, 2 yearlings from Patagonia that were satellite tracked simultaneously with subadult males during the postmolting season (January–August—C. Campagna, pers. obs.) dispersed widely into the deep open ocean close to South Georgia. This possibly could be a way of dealing with competition with conspecifics, as in Macquarie Island where yearlings remain near the colony whereas adult females and older juveniles forage in more-productive areas located south of the Antarctic Polar Front (Bradshaw et al. 2003; Field et al. 2005; Hindell et al. 1991). The continental shelf around Macquarie Island is an area of more than 1,000 km<sup>2</sup> of sea floor that drops steeply to almost 1,000 m

in depth (Green and Burton 1993). In such an environmental context juveniles have shown increased diving effort (54% of the dives were extended dives—Irvine et al. 2000). Inexperienced and physiologically limited juveniles from Península Valdés could forage over the shallow and highly productive Patagonian Shelf during postresting periods when most of adults and older juveniles are ashore. The presence of the large and highly productive Patagonian Shelf could help explain why Península Valdés is the only colony exhibiting a positive increment of the population in contrast with other southern colonies of elephant seals (Campagna and Lewis 1992; Lewis et al. 2004), where comparatively narrow and less productive shelves can force juveniles to increase their diving effort, with potential consequences for their survival (Irvine et al. 2000).

## RESUMEN

En Patagonia, la plataforma somera frente a Península Valdés restringe la profundidad de los buceos de los elefantes marinos del sur (*Mirounga leonina*) a menos de 100 m en la mayor parte de su extensión, un comportamiento inusual para estos animales. Fuera de la plataforma, deben buscar su alimento a lo largo de la columna de agua donde las profundidades son > 1000 m. Comparamos los patrones de buceo de diez juveniles de Patagonia equipados con registradores de luz y temperatura, para evaluar diferencias en el esfuerzo de buceo (medido como duraciones mayores al límite aeróbico) en áreas de la Plataforma Patagónica y del océano adyacente. La Plataforma Patagónica, un ambiente en el que el esfuerzo de buceo de los juveniles fue menor, también es un área comúnmente utilizada por animales de mayor edad. Estos posiblemente desplazan periódicamente a los juveniles fuera de la plataforma donde se ven forzados a incrementar su esfuerzo de buceo.

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