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DETECTING BIOLUMINESCENCE WITH AN IRRADIANCE TIME-DEPTH RECORDER DEPLOYED ON SOUTHERN ELEPHANT SEALS

While at sea, elephant seals (*Mirounga* spp.) spend 90% of their time underwater, at mean depths of 400–500 m while foraging during both daytime and nighttime (Le Boeuf 1994). Although most surface light is lost before reaching these depths, elephant seals have adaptations to low light levels that suggest visual predation. They have large eyes with a wide range of pupillary dilation (Levenson and Schusterman 1997), rapid adjustment to darkness (Levenson and Schusterman 1999) and a retina that has a peak sensitivity shifted to the blue-green (Lythgoe and Dartnall 1970, Carlson and Le Boeuf 1998). At depths where seals spend most of their time, bioluminescence is the main source of light (Seliger and McElroy 1965, Young 1983, Widder *et al.* 1989, Case *et al.* 1994), and it is produced at levels and wavelengths (Herring 1983, Haddock and Case 1999) that can be detected by the elephant seal eye (Le-

venson and Schusterman 1997, 1999). A visual predator foraging in deep waters may then be cueing on bioluminescent prey (McFarland 1971, Le Boeuf *et al.* 1988) or may use stimulated bioluminescence for indirect detection of prey (Mensinger and Case 1992, Fleisher and Case 1995).

We deployed irradiance-time-depth recorders (I-TDRs) on female southern elephant seals, *M. leonina,* from Península Valdés, Argentina, (Campagna *et al.* 1993) in an attempt to sample the luminescent field to which elephant seals were exposed during dives. Previous work has interpreted the foraging behavior of elephant seals indirectly from depth, water temperature, swim speed, and underwater sound data (*e.g.,* Le Boeuf *et al.* 1988, 1989, Hakoyama *et al.* 1994; Fletcher *et al.* 1996; Crocker *et al.* 1997; Burgess *et al.* 1998; Campagna *et al.* 2000). Our results indicate that diving elephant seals are exposed throughout the water column to irradiance, which most likely originates in bioluminescent organisms. This paper is an innovative approach to the understanding of diving behavior. We acknowledge that our results are limited by technical difficulties, which need to be overcome to examine the link between bioluminescence and seal foraging behavior. This work is a step towards that goal.

Five adult females ready to wean their pups were immobilized with an intramuscular injection of Telazol (Aveco Co. Inc., IA; Campagna *et al.* 1998) in October 1997 ($n = 3$) and 1998 ($n = 2$). An I-TDR was positioned between the shoulders on the dorsal midline of each animal and attached with marine epoxy (Campagna *et al.* 1998). The instruments consisted of a programmable data logger (Tattletale Lite model L-512F, Onset Computer Corporation, MA) enclosed in an aluminum housing. Total weight of the instrument package was 1.4 kg in air and 0.4 kg in water. The instrument had 1 MB of pseudostatic RAM. Analog sensory circuitry was interfaced with the data logger to measure depth, water temperature, swim speed, and irradiance. Diving depth (resolution of 0.6 m) was measured with a pressure transducer (model PA-7, Keller PSI, Oceanside, CA) located in the outside wall of the housing. Swim speed was measured by tallying the revolutions of a turbine (Logtron Impuls, Flasch Electronic GmbH, Lerchenstrasse 5, München, Germany) located on top of the housing. A minimum swim-speed calibration was obtained following Blackwell *et al.* (1999). Irradiance was detected with three photodiodes sensitive to visible light with suppressed IR sensitivity (model S1227–1010BR, spectral response range of 320–1,000 nm; Hamamatsu Photonics K. K., Solid State Division 1126–1, Ichino-cho, Hamamatsu City, 435–91, Japan). Each diode had a surface area of 1 cm^2 and was housed inside the aluminum case. Photodiodes were connected in parallel to increase the sensitivity of the system. Current generated by incident irradiance was amplified with a two-stage operational amplifier circuit with a gain of 10^{10} V/A and a flat frequency response in the band 0–10 Hz. The amplifier was tested for linear response within sampled voltages with controlled current sources. The response linearity of the photodiodes is guaranteed by the manufacturer; low temperatures lead to improved linearity. Irradiance detection occurred through a round polycarbonate window 0.5 cm thick and 3.3 cm in diameter. Trans-

mittance of the window, as determined with a light spectrophotometer, was 80% at λ = 480 nm. No color filter was interfaced with the light-sensitive elements.

All three variables were recorded and stored in memory every 5 sec. A peak-detector circuit was designed to hold the highest irradiance value detected during the sampling interval and relay it to the data logger for permanent storage. Sensors detected a wide range of wavelengths of visible light. However, the most common light spectra of marine bioluminescent organisms occur within the range of blue-green wavelengths (λ = 440–506 nm; Haddock and Case 1999 and references therein). In an attempt to produce a theoretical estimate of levels of recorded irradiance we calculated that saturation (at λ = 480 nm) occurred at and above 5.02×10^{-4} μWatt/cm^2 (see Appendix 1). Likewise, we defined a conservative operational baseline at a calculated irradiance of 9.8×10^{-5} μW/cm^2 for the same wavelength. The defined baseline gives more relative weight to stronger signals than the actual darkness for the sensors, calculated at 8.0×10^{-5} μW/cm^2. Because the distance from the source, the angle of recording relative to the source, and the duration of the light flash were unknown, actual levels of irradiance in the environment were difficult to interpret. Consequently, signals were normalized to arbitrary units on a linear scale where 0 = baseline, 5 = defined baseline, and 25 = saturation. Because of this design, we cannot relate the irradiance samples to the light produced by an individual organism (only at λ = 480 nm would 0, 5, and 25 translate into the above calculated levels in μWatt/cm^2). Rather, samples should be seen as a relative measure of the luminescent field surrounding the recorder.

To test the effect of surface irradiance on the sensors we submerged one instrument to a depth of 100 $\pm$ 6 m for 150 h. No records were obtained above actual baseline levels (0) during 11.6 night hours during the dark part of the lunar cycle. Moonlight was detected as irradiance values within the dynamic range of the instrument. Virtually all daylight samples resulted in saturation of the sensors. When the instrument was deployed on a diving seal, saturation in midday dives occurred down to 300 m during descent and 400 m during ascent (sensors pointing up). These depths represent maximum values regarding saturation of the sensors.

In an attempt to eliminate the confounding effect of background surface irradiance, we restricted our analysis to night samples during the dark part of the lunar cycle and to depths >100 m. Time of sunrise and sunset (as well as moonrise) were clearly identifiable in the records (*e.g.,* Fig. 1a), and gave us an estimate of local midnight as well as solar noon (longitudes calculated from the time of solar noon were well within the known distribution at sea of post-breeding foraging females, see Campagna *et al.* 1998). A night sample was any sample occurring within three hours before or after local midnight. When the moon was visible, the selected time window for night samples was shortened to eliminate records obtained after moonrise. Underwater flashes were often more intense at depth under the selective sampling conditions for darkness outlined above, than when the animal was at the surface (Fig. 1b).

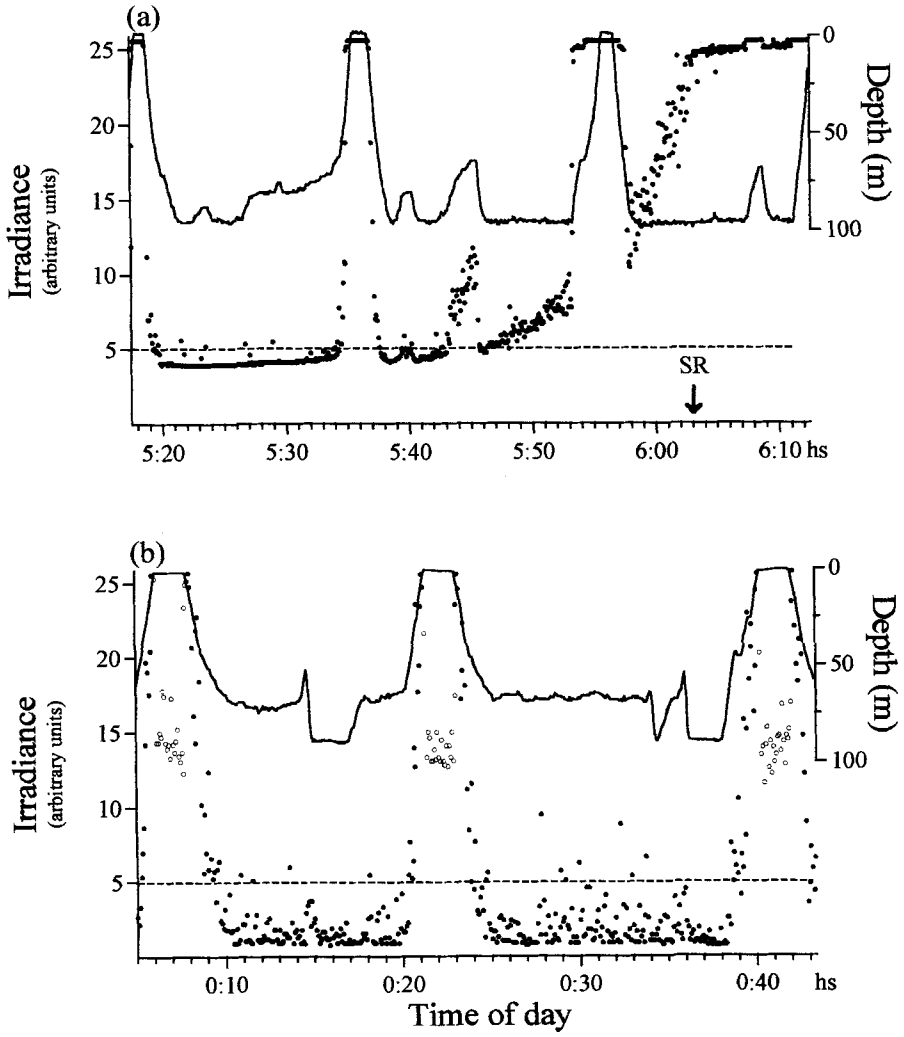

Figure 1. (a) Depth as function of time for shallow dives and associated irradiance samples (measured in relative arbitrary units) obtained 15 October 1997 for female PB-K. Irradiance samples reflected onset of dawn. SR: sunrise time. (b) Two dives on the continental shelf showing that some flashes detected during descent and ascent phases were above levels of irradiance recorded at surface (open circles). This example indicated that I-TDRs detected flashes above maximum possible background value of down dwelling light.

During these selected sampling periods, when the seal was in darkness due to its depth, the time of day and lunar cycle, the light detected was considered to come from bioluminescence. Only a few examples were taken from outside this restricted data set to illustrate specific aspects of the results.

Within this stringent subset of data, we studied the variation in the "flash sample" (FS) rate per minute, as a function of dive depth and swimming speed.

A flash sample is a sample with an irradiance value of at least 5 and below 25 (*i.e.,* above baseline but below saturation). Because of the sampling protocol there could therefore be 0–12 FSs per minute. We assume that the FS rate is a reflection of the environment's bioluminescence potential. Least-square linear regression analyses were conducted on FS rate *vs.* swim speed for samples obtained at five depth intervals of 50 m each (0–50 m, 50–100 m, 100–150 m, 350–400 m, and 400–450 m).

Three instruments were recovered encompassing a total of 36 d at sea (16.5 d off the continental shelf) and 2,617 dives (Table 1). All recorded dives for female PB-J (n = 1,013) occurred on the shallow continental shelf (Table 1) and were exposed to surface irradiance. Her record was therefore excluded from the analysis. The other two females (PB-K and PB-L) provided 24 h of data within the restricted subset of samples.

The FS rate decreased as a function of depth with no abrupt changes (Fig. 2). Flashes were detected up to about 1,000 m—near the maximum dive depth for the studied seals (Fig. 3; dives in the latter figure occurred at a time of day excluded from the restricted data set, therefore the irradiance samples were not included in the analysis).

Almost uninterrupted movement while the animals were underwater limited the opportunity to compare flashes between active and resting phases of a dive. The few dives with pauses in swim speed occurred mostly during daylight hours, during periods of the night with a moon, or while seals were traversing the shallow continental shelf (*e.g.,* Fig. 4a). The latter dives were therefore excluded from the overall analysis. However, seven of PB-L's dives, that occurred at night over the continental shelf, are worth special consideration. These dives (50–60 m deep) contained a middle section during which swim speed was close to 0 m/sec. Swim speed preceding (descent) and following (ascent) these sections was 0.9 ± 0.4 m/sec. During the pauses (that totalled 43 min), the number of flashes per minute above operational baseline level was 0.38, as compared to 8.8 and 7.6 during one-minute periods directly preceding or following the pause. Three dives that occurred within an hour of the above but contained no pauses in swim speed showed a mean of 7.2 flashes per minute in 27 min at 50–60 m (*i.e.,* the animal was not ascending or descending). Similar results were found in three C dives of seal PB-K (see Le Boeuf *et al.* 1992 and Crocker *et al.* 1997 for a description of C dives). During these C dives, the seal transitioned from a mean swim speed of 1.3 ± 0.5 m/sec during the first leg of the dive to a drifting speed close to 0 m/sec, and back to 1.3 ± 0.3 m/sec during the ascent phase. FS rates were 5.3, 0.6 and 3.8 records/min before, during, and after the drifting phase, respectively. In a comparison restricted to samples obtained at similar depths (200–250 m), FS rates were 2.8, 0.6, and 2.0 records/min, respectively. The general relationship between swim speed and irradiance was analyzed within the restricted data set for female PB-K (who showed more variation in swim speeds than PB-L; mean = 1.8 m/sec, range = 1.4–2.4 m/sec *vs.* 1.5 and 1.4–1.8 m/sec, respectively). The FS rate increased as a function of increasing swim

Table 1. Summary statistics from diving records of post-breeding female southern elephant seals on and off the continental shelf.

		On shelf								Off shelf							
Female	First sampling day	No. dives	Days record-ed	Mean dives/h	Mean depth (m)	Max. depth (m)	Mean dur. (min)	Max. dur. (min.)	Mean surf. int. (min)[a]	No. dives	Days record-ed	Mean dives/h	Mean depth (m)	Max. depth (m)	Mean dur. (min)	Max. dur. (min)	Mean surf. int. (min)
PB-J	6 Oct 97	1,013	12.1	3.4	98	108	14.5	28	2.2	—	—	—	—	—	—	—	—
PB-K	14 Oct 97	158	1.9	3.4	87	175	15.6	24	1.5	594	10.2	2.4	605	1,036	22.6	41	2.2
PB-L	8 Oct 98	460	5.6	3.4	92	146	15.9	27	1.4	392	6.2	2.6	534	899	20.7	37	2.0
Total		1,631	19.6							986	16.5						
Mean		543	6.5	3.4	91	143	14.3	26.3	1.9	493	8.2	2.5	576	967	21.8	39	2.1
SD		354	4.2	0.0	25	27	4.5	1.8	0.6	101	1.9	0.1	171	68	4.2	2.1	0.3

[a] Excludes surface intervals longer than 5 min.

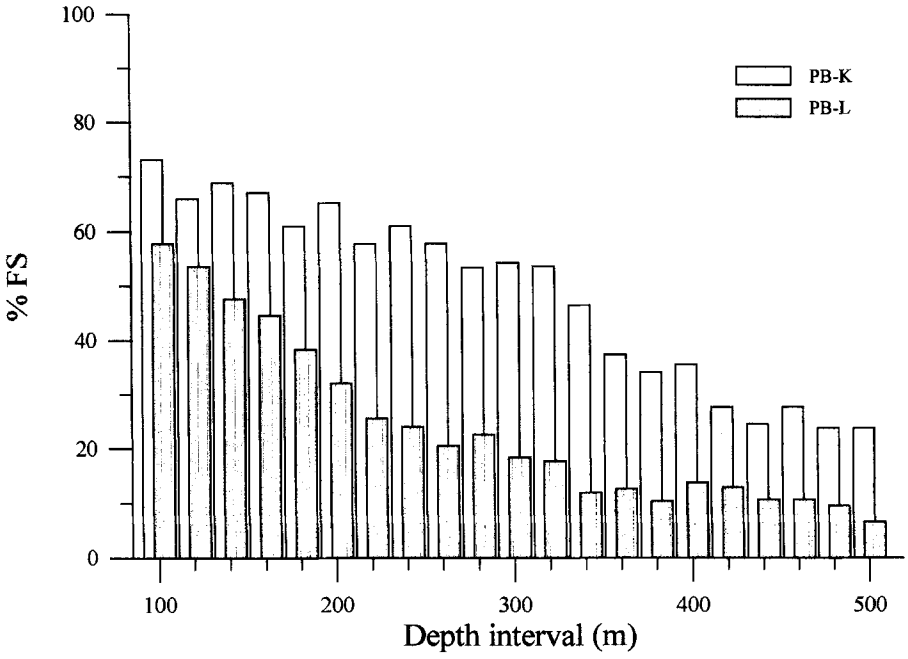

Figure 2. Percent of flashes (FS) above operational baseline level (see Methods) as function of 20-m dive depth intervals for two females. Column bars based on mean (± 1 SD) of 463 ± 231 samples for PB-K and 915 ± 381 samples for PB-L.

speed for a set of depths ranging from shallow to deep waters (Fig. 4; all significant slopes and values of regression lines are given in figure legend).

The FS rate increased in the transition from the continental shelf to deep waters. Female PB-K approached the shelf slope at night and crossed it at dawn. Figure 5 shows 20 dives, 17 on the shelf and three on the shelf slope. The dive marked with an asterisk corresponds to the moment when the FS rate starts increasing, about 2.5 h before sunrise. There was a significant increase in the FS rate between the five dives preceding and following the asterisk dive (Chi-square test = 170, $P < 0.01$; asterisk dive excluded from the analysis). All 10 dives were of similar depth and duration, and had a similar swim-speed pattern and shape. The period around sunrise is visible on the irradiance record and coincided with the last dives on the shelf. However, the increase in FS rate was apparently not due to the effect of surface irradiance, as the proportion of records near saturation levels is similar between the two sets of five dives (90 samples in 110 min *vs.* 89 samples in 105 min, respectively).

We interpret the flashes recorded by the I-TDR mainly as mechanically stimulated bioluminescence triggered by the almost constant motion of the females. Swimming movements of dolphins, cephalopods, fish, mysids, and shrimp, as well as the motion of man-made instruments to detect light, are known to stimulate bioluminescence (Widder *et al.* 1989, Rohr *et al.* 1998).

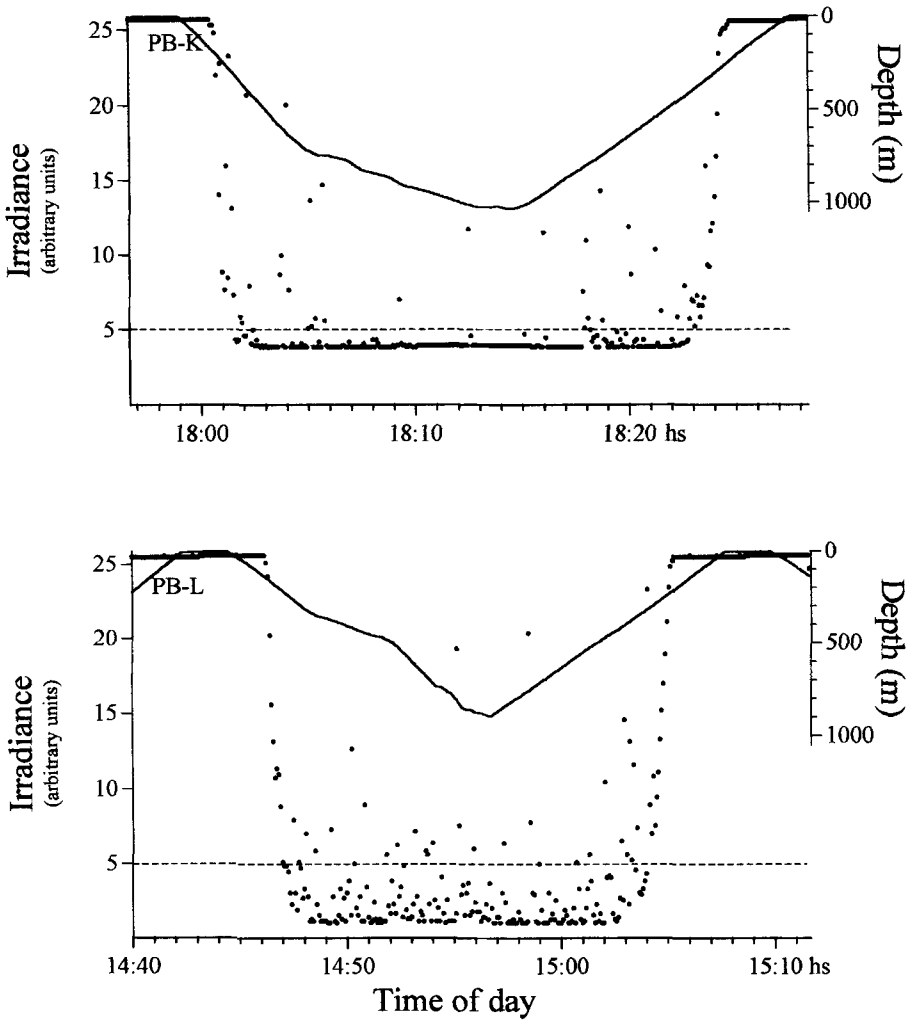

Figure 3. Flashes associated with deepest dives for each of two females that travelled beyond continental shelf (PB-K and PB-L). Flashes above defined baseline level (Dotted lines) occurred at different depths in water column, including near bottom of dive at 900–1,000 m.

It is likely that the source of the light recorded by the I-TDR are organisms or their secretions located very close or directly in front of the photodiodes. We cannot then say that what the seal sees is identical to what the instrument recorded. However, the mechanical disturbance and the stimulated bioluminescence caused by the instrument will also be elicited by the movement of seals and their potential prey, and would be related to abundance of bioluminescent organisms.

The increase in FS rate when approaching the shelf slope suggests an increase in the density of bioluminescent organisms. This is consistent with the

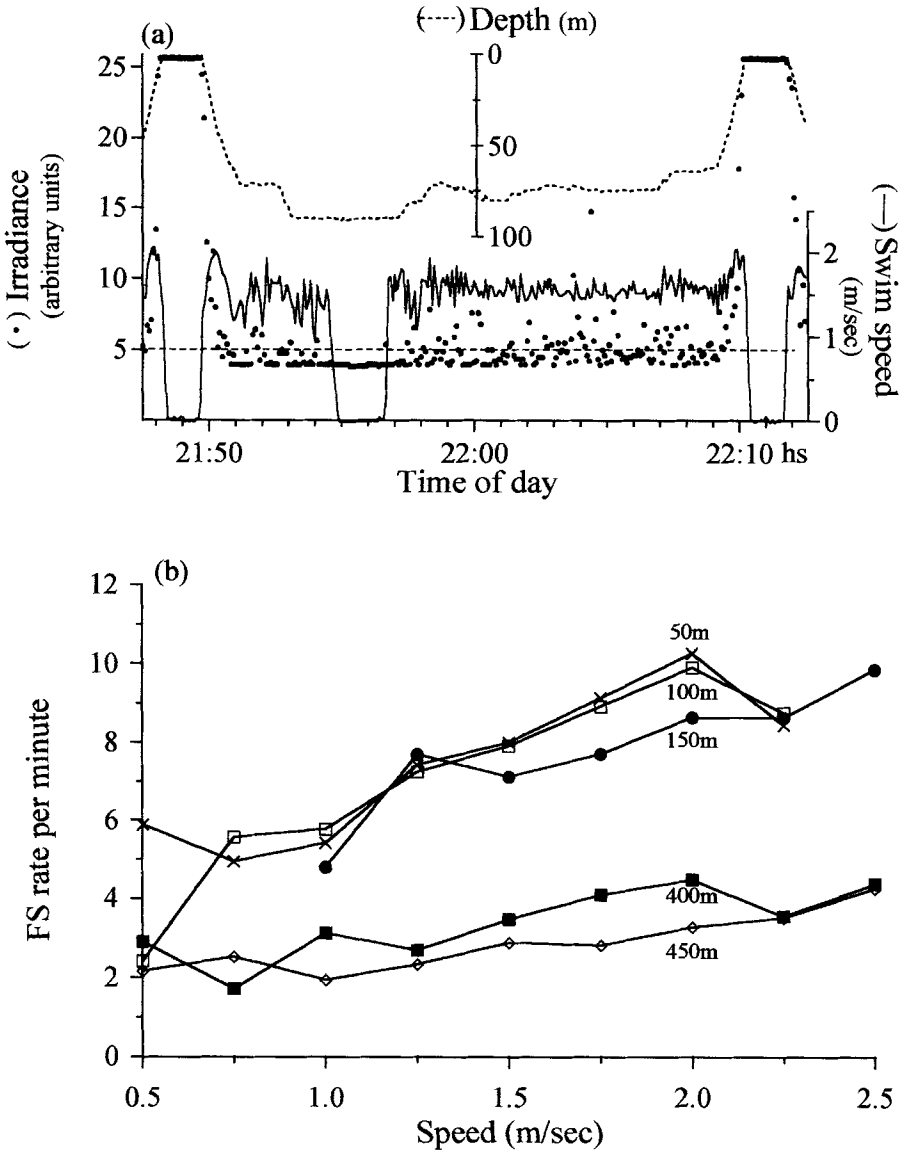

Figure 4. Flashes as function of swimming speed. (a) One dive on continental shelf for female PB-K showing that during pause lasting about 90 sec (swimming speed close to 0 m/sec) irradiance samples did not occur above baseline level of detection. This example suggests that flashes originated in mechanically disturbed conditions during swimming. (b) Variation in flash sample (FS) rate per minute as function of swimming speed for female PB-K. Data shown for five 50-m depth intervals (upper values of intervals indicated in legend). Line equations obtained by least-square linear regression analysis of FS on swim speed were: 50 m: $y = 2.7x + 3.8$, $r^2 = 0.76$; 100 m: $y = 3.6x + 2.1$, $r^2 = 0.85$; 150 m: $y = 2.7x + 3.1$, $r^2 = 0.82$; 400 m: $y = 1.0x + 1.8$, $r^2 = 0.64$; 450 m: $y = 1.0x + 1.4$, $r^2 = 0.82$. All slopes statistically significant ($P < 0.05$).

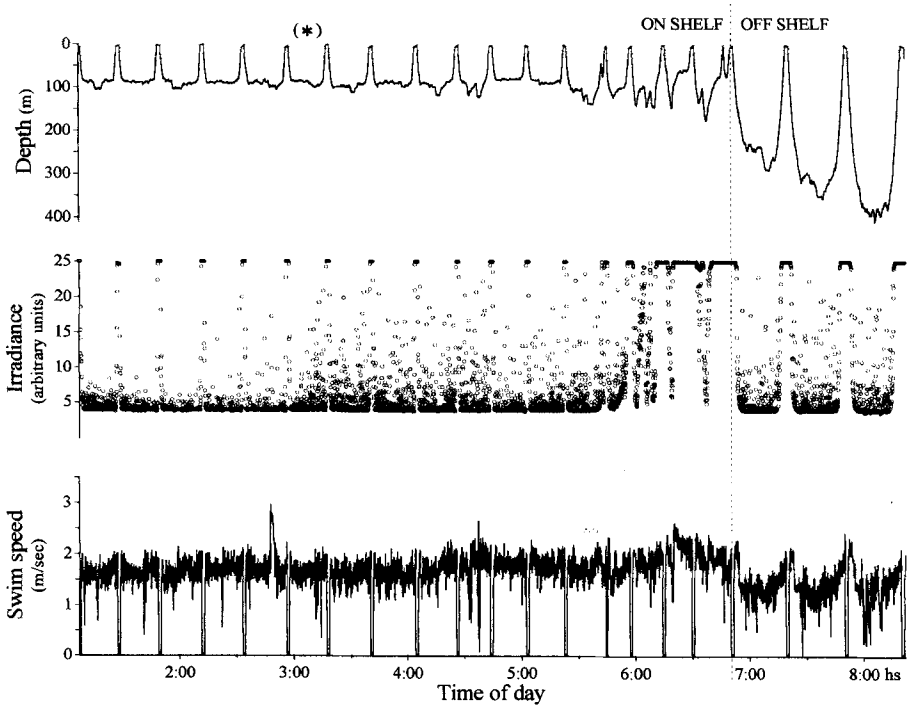

Figure 5. Transition from continental shelf to deep waters for female PB-K. Asterisk indicates dive in which number of flash samples above baseline sensitivity of sensors increased compared to previous dives. Sunrise occurred during last dives on shelf, immediately before animal arrived at shelf slope.

high productivity associated with the Malvinas Current (Martos and Piccolo 1988, Podestá 1990, Carreto *et al.* 1995). It is not known if seals cue in on the amount of luminescence to detect productive areas (Case *et al.* 1994), but changes in irradiance may well be an additional factor of potential predatory significance (Widder *et al.* 1989). Likewise, changes in the rate of detected flashes with depth could be due to variations in the distribution, density, and species composition of bioluminescent organisms in the water column (Young 1983). The sources of bioluminescence could not be determined, but it is likely that most flashes recorded deeper than 100 m were not originated in phytoplankton (Widder *et al.* 1989).

This study is a step towards understanding the visual information that may be used by diving elephant seals as they travel through the aphotic environment, and how this information relates to foraging and orientation towards a potential prey. Methodological and instrumentation constraints preclude determining, at this stage, whether the bioluminescent environment provides useful predation information to the seals. However, our results (1) provide an estimate of bioluminescent activity in the waters through which elephant seals dive, (2) demonstrate the feasibility of using elephant seals as autonomous

samplers of the bioluminescent environment, (3) show that seals are exposed to variable ranges of luminescence throughout their diving depths, and (4) suggest that seals have access to information on density and distribution of bioluminescent organisms that may indicate prey availability. This study strengthens Levenson and Schusterman's (1999) conclusions, based on visual sensitivity studies in laboratory conditions, that predation in elephant seals may be facilitated by bioluminescence. Future technical improvements should be aimed at decreasing the size of the instrument to allow deployment on the seal's head, increasing control over crucial variables by changes in housing design (*e.g.,* shear stress, volume of water sampled, positioning of the sensors in relation to surface-incident irradiance), and allowing conditional sampling protocols. The I-TDR is a relatively cheap instrument that has the potential to shed light on predatory strategies used by diving seals. It may also provide hard-to-get information on the stratification of bioluminescent organisms in time and space (Case *et al.* 1994), particularly at depths beyond conventional profiling bathyphotometers.

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APPENDIX 1.

Theoretical estimate of thresholds of the I-TDR.

$$0.3\frac{A}{W/cm^2} \times 3 = 0.9\frac{A}{W/cm^2} \quad (1)$$

$$0.9\frac{A}{W/cm^2} \times 10^{10}\frac{V}{A} = 0.9 \times 10^4\frac{V}{\mu W/cm^2} \quad (2)$$

$$0.9 \times 10^4\frac{V}{\mu W/cm^2} \times 0.8 = 0.72 \times 10^4\frac{V}{\mu W/cm^2} \quad (3)$$

$$\frac{3.63V}{0.72 \times 10^4\frac{V}{\mu W/cm^2}} = 5.02 \times 10^{-4}\ \mu W/cm^2 \quad (4)$$

(1) Current produced with three photodiodes.
(2) Operational amplifier gain.
(3) Effect of polycarbonate window.
(4) Upper limit of sensitivity.
Notes:
Diode photosensitivity (based on the spectral response provided by the manufacturer): 0.3 A/(W/cm^2) at λ = 480 nm.
Number of diodes in parallel: 3.
Gain of circuitry: 10^{10} V/A.
Transmittance of polycarbonate window (at λ = 480 nm): 80% or 0.8.
Upper limit of voltage range from circuit: 3.63 V.

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SURVIVORSHIP OF CAPTIVE SOUTHERN SEA OTTERS

Recent range-wide surveys of the population of southern sea otters *(Enhydra lutris nereis)*, which extends seasonally from Refugio State Beach, CA, to Pillar Point, CA, suggest that the population is declining. In particular, the decline is attributed to the fewer numbers of sea otters counted in the central portion