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RESEARCH ARTICLE

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Using time-depth-light recorders to measure light levels experienced by a diving marine mammal

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Abstract This study examined the feasibility of using time-depth-light recorders (TDLRs) to measure light levels experienced by a diving marine mammal. TDLRs were deployed on ten female Antarctic fur seals (*Arctocephalus gazella*) at Bird Island, South Georgia (54°00′S 38°02′W) in the 1994–1995 austral summer. Depth and light measurements were made during 11 foraging trips which lasted on average (±SE) 7.1±0.7 days. A total of 25,657 dives were recorded with a mean dive depth and duration of 18.0±3.6 m and 49.5±6.9 s, respectively. Depending on time of day, fur seals experienced on average 6–57% of the surface illumination when diving. Illuminance ranged from full sunlight (10^4 lx) at the surface to minimum starlight (10^{-6} lx) at night and during deep daytime dives. TDLRs recorded strong light attenuation in the top 50 m of the water column. The mean attenuation coefficient was $0.140 \pm 0.014\ \mathrm{m}^{-1}$, which was in the upper range of values measured by ship surveys at South Georgia. These findings suggest that TDLRs may be a useful method of obtaining information on the bio-optical properties of the ocean where fur seals forage. Development of sensors with appropriate spectral sensitivity and suitable resolution at low light levels is recommended to improve the capability of these devices for the study of marine mammals.

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Introduction

Time-depth recorders (TDRs) have provided detailed information on the diving behaviour of a wide range of pinnipeds (Boyd and Croxall 1996; Le Boeuf et al. 1996). The development of smaller data-loggers with additional sensors and increased memory has extended the capability of these devices to record a variety of additional variables, including temperature and swim speed (e.g. Ponganis et al. 1990; Boyd et al. 1995; McCafferty et al. 1999). TDRs are often fitted with light sensors to measure day length as a means of estimating geographical position (DeLong et al. 1992; Hakoyama et al. 1994; Le Boeuf et al. 1996) and more recently as a means of recording light levels when diving (Baird et al. 2001). Measurements of the intensity and spectral properties of light at depth could also give insights into the way seal vision is adapted for underwater foraging and may provide a method of estimating plankton concentration and hence primary productivity of waters where marine mammals feed (Smith and Baker 1978a; Mitchell and Holm-Hansen 1991a; Fenton et al. 1994).

Given the current advances in dive recorder technology the aim of this study was to examine the feasibility of using time depth light recorders (TDLRs) to determine the light levels experienced by a marine mammal when diving and to assess the extent to which questions relating to pinniped vision and bio-optical properties of the ocean may be addressed with these instruments.

Materials and methods

Deployments

TDLRs (Mk5 and Mk6 Wildlife Computers, Redmond, Wash., USA) were deployed on ten female Antarctic fur seals between 24 November 1994 and 19 February 1995 at Bird Island, South Georgia (54°00′S, 38°02′W). Previously tagged females suckling healthy pups were captured and restrained using standard methods (Gentry and Holt 1982). TDLRs were glued directly onto the mid-dorsal fur using quick setting epoxy adhesive (RS Ltd, Corby, Northants, UK). Females were also fitted with a 40-g, 165-MHz radio-transmitter (Sirtrack, Havelock North, New Zealand) to relocate individuals when they returned ashore. Body mass (±0.5 kg) and nose–tail length (±0.5 cm) were recorded and females were returned together with their pups to their suckling location. On recapture, females were measured and the TDLR and radio-transmitter were carefully removed by clipping the fur beneath the device.

TDLRs recorded depth (±1 m) and light (uncalibrated units) at 5-s intervals. Depth measurements were made by a pressure transducer calibrated by the manufacturer. Light was measured by a photodiode (BPX 63 Siemens Microelectronics, Cupertino, Calif., USA). The photodiode had a spectral sensitivity of 350–1,100 nm with peak sensitivity at 800 nm (Fig. 1). On recovery of TDLRs, data were transferred to computer and decoded using custom written software to produce an ASCII list of depth and light readings, as well as a summary of individual dives (Boyd et al. 1997).

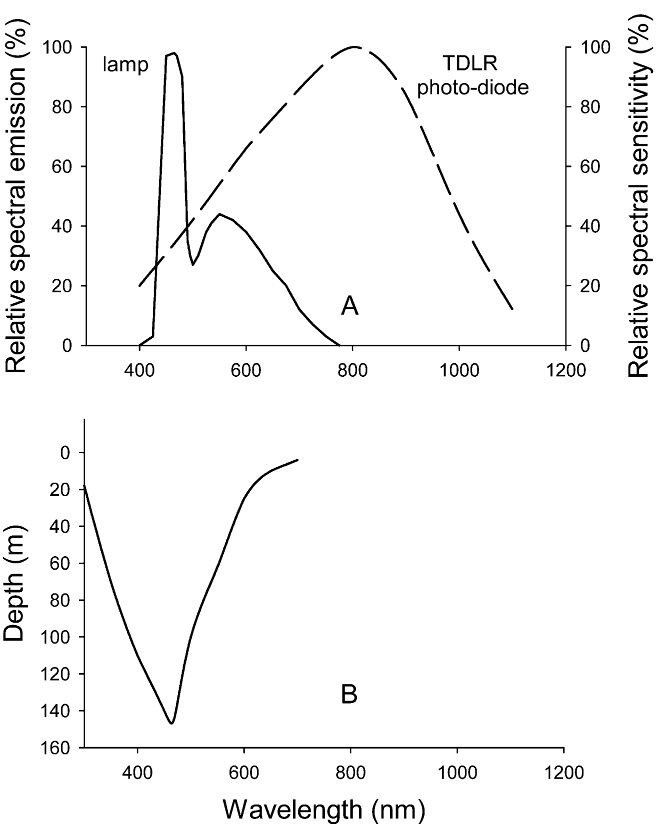


Fig. 1 Relative spectral emission (%) of the tungsten halogen calibration lamp and the relative spectral sensitivity (%) of the TDRL photodiode in relation to light of different wavelengths (nm) (**A**). This is compared with the depth (m) of penetration of light in clear oceanic waters to 1% of the surface light level (**B**) (Lalli and Parsons 1993)

The light sensor on a Mk5 and Mk6 TDLR was calibrated against a tungsten–halogen monochromatic fibre optic lamp (400–750 nm, model KL1500, Schott Fibre Optics, Doncaster, UK). Light level was varied from 1.4 lx to 119 klx using neutral density filters (HV Scan, Solihull, UK). Illumination (±0.1 lx, 400–700 nm peak 550 nm) was recorded on a digital light meter (Model TES1332, TES Electronic Corporation, Taipei, Taiwan). Transmittance was determined by dividing the illuminance at depth z (I_z) by the maximum hourly illuminance (I_o) recorded at the surface (≤ 1 m). To avoid bias from readings that were below the sensitivity threshold of the instrument, TDLR readings of zero light were excluded from the analysis. The transmittance for each depth was averaged for each deployment. The diffuse attenuation coefficient, K_d (m^{-1}) was the gradient of the least squares regression line of ln (I_z/I_o) against depth (≤ 50 m). Data handling and statistical analysis were carried out using SAS version 6.11 (SAS Institute, Cary, N.C.). Local time (LT) was approximately equal to GMT −2 h.

Ship surveys

During British Antarctic Survey cruise JR11 of the R.R.S. "James Clarke Ross", an undulating oceanographic recording (UOR) system was deployed. The instrumentation included a photosynthetically active radiation (PAR) irradiance meter (Biospherical Quantum Cosine Profiling Sensor, Biospherical Instruments, San Diego, Calif., USA). The PAR meter was calibrated to convert voltage to μEinsteins m^{-2} s^{-1}. Data were obtained from two surveys: on 18 January 1996 at 0747–1745 hours, and on 19 February 1996 from 1806 to 2116 hours LT. The first survey was part of an oceanographic survey to the north of Bird Island from inshore and across the continental shelf. The second survey took measurements across the shelf.

Light intensity from the PAR sensor was converted to illuminance (lx) where 1 Wm^{-2} was approximately equal to 4.2 μEinsteins $m^{-2}s^{-1}$ at a wavelength of 550 nm (Lalli and Parsons 1993) and by assuming for simplicity an arbitary luminous efficacy of 100 lumens (lm)/W. The relationship between illuminance and depth was determined by taking the average illuminance at each depth for each hour. As measurements of illuminance were not obtained at the surface, surface illumination was estimated by linear regression of ln PAR against the UOR depth measurement ($R^2 > 0.91$, $P < 0.0001$ in all cases).

Solar radiation at the surface

The global solar illuminances averaged over all cloud conditions and in cloud-free conditions for November–February were obtained using radiation algorithms for South Georgia (Gardiner 1987).

Results

Calibration of TDLR light sensor

The TDLR output showed a saturating response for the detector with large increases in applied irradiance resulting in progressively smaller increases in output (Fig. 2). The regression equation for the Mk5 TDLR was: output $=7.69$ ln (lx) $+$ 91.5 ($R^2=0.99$ $F_{1,18}=$ 16,326 $P<0.0001$). The calibration of the Mk6 TDLR was also equal to: output $=7.69$ ln (lx) $+$ 91.5 ($R^2=0.99$ $F_{1,16}=15{,}985$ $P<0.0001$). Although TDLR sensors showed a log-linear response over the calibration range, TDLRs placed inside a light-proof bag gave a reading of zero that did not lie on the calibration line. This indicated that there was a light threshold at which the sensor did not operate. Therefore zero readings were assumed to be less than or equal to the calibration offset of 7×10^{-6}lx.

Deployments on fur seals

Deployments were made on ten females using three Mk5 and two Mk6 devices during 11 foraging trips which lasted on average (±SE) 7.1±0.7 days (Table 1). Data were obtained for a total of 59.1 days (80% of time at sea) and included a total of 25,657 dives. The mean dive depth was 18.0±3.6 m and dive duration was 49.5±6.9 s.

TDLRs provided a detailed record of light levels experienced by fur seals throughout a number of complete foraging trips (Fig. 3A) and clearly showed the diel pattern of illumination and record of diving (Fig. 3B). At the scale of individual dives, changes in illumination matched changes in depth. In comparison, when fur seals remained on the surface, illumination was highly variable (Fig. 3C).

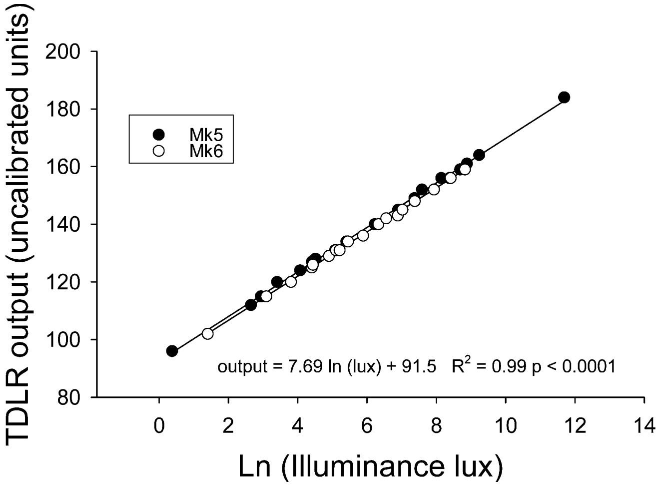


Fig. 2 The relationship between the output from *MK5* and *Mk6* TDLRs and ln illuminance (lux) calibrated with lamp (400–750 nm)

Table 1 Body mass, age and foraging behaviour of female Antarctic fur seals fitted with time-depth-light recorders (TDLRs) in this study. The different TDLRs are identified by TDLR type (Mk5 or Mk6) and serial number of the device. *Asterisk* indicates two sequential trips recorded from this female

Tag	Body mass (kg)	Age (years)	TDLR type	Start of foraging trip	Trip duration (days)	% Trip recorded	Num. of dives	Mean depth (m)	Mean duration (s)	Max. depth (m)	Max. duration (s)
W1206	35.8	10	Mk5 (94–225)	27 November 94	10.0	25	844	13.5	42.1	83	195
W1308	42.5	–	Mk5 (94–226)	25 November 94	11.1	21	611	3.8	16.2	51	130
W1470	40	–	Mk5 (94–224)	01 December 94	3.8	66	953	12.2	43.4	85	205
W1765	50.5	15	Mk6 (94–170)	12 February 95	7.3	100	2,214	15.4	52.1	113	235
W2301	43.8	13	Mk6 (94–170)	21 January 95	6.9	100	2,434	33.8	83.0	138	270
W2379*	34.5	15	Mk6 (94–169)	20 January 95	4.6	100	1,503	36.9	83.2	131	185
W2379*	–	–	Mk6 (94–169)	26 January 95	4.5	85	1,020	35.4	79.0	172	230
W2921	41.5	10	Mk6 (94–169)	21 February 95	7.3	85	3,898	7.6	30.0	159	225
W3805	33.5	–	Mk6 (94–170)	21 February 95	7.1	100	4,574	8.6	28.8	138	280
W3821	37.5	4	Mk6 (94–169)	09 February 95	7.9	100	4,746	11.8	43.0	189	255
W3867	34.5	8	Mk6 (94–170)	01 February 95	7.8	100	2,860	19.1	43.1	120	205
mean Mean ± SE	39.2 ± 1.5	11.2 ± 1.4		17 January 95	7.1 ± 0.7	80 ± 9.1	2,332 ± 458	18.0 ± 3.6	49.5 ± 6.9	125.4 ± 12.4	219.5 ± 12.8

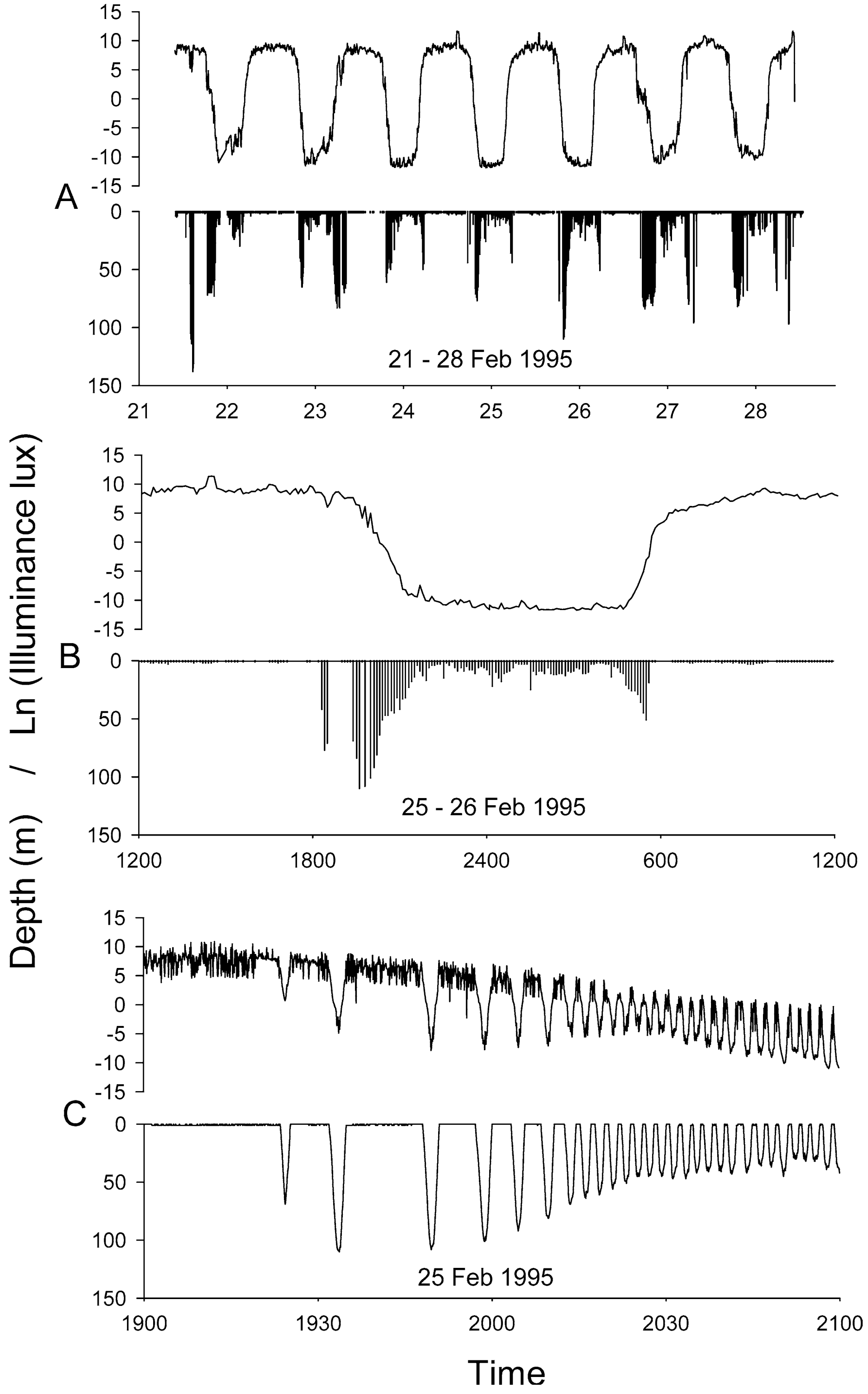


Fig. 3A–C The TDLR record from female W3805 fitted with a Mk6 TDLR from 21 to 28 February 1995. Changes in illuminance during diving are shown at the scale of: **A** the complete foraging trip, **B** a day and, **C** a 2-h period. Ln illuminance (lux) is plotted on the top and dive depth (*m*) on the bottom axis of each diagram

The uncalibrated output from the TDLR ranged from 0 to 195, which represented a range in illuminance from $\leq 7\times10^{-6}$ lx to 690 klx. The maximum illumination was greater than a mean of 100 klx for the modelled solar illuminance at sea in cloud free conditions in mid-December at South Georgia. Illuminances that were greater than the maximum calibration value represented only 0.37% of the total number of light readings. When fur seals were within 1 m of the surface the light levels recorded were similar to those modeled from meteorological data for at South Georgia (Fig.4). The change in light level experienced by fur seals at depth throughout the 24-h period followed the pattern of daylight, and fur seals were foraging at mean light levels between 10^4 during the day and 10^{-3} lx at night. On average fur seals experienced $22\pm3.0\%$ ($n=24$) of the surface illumination when diving. This ranged from 6% at 2300 hours LT to 57% at 1100 hours LT. The minimum light level reached was 10^{-6} lx throughout the middle of the night (Fig 4).

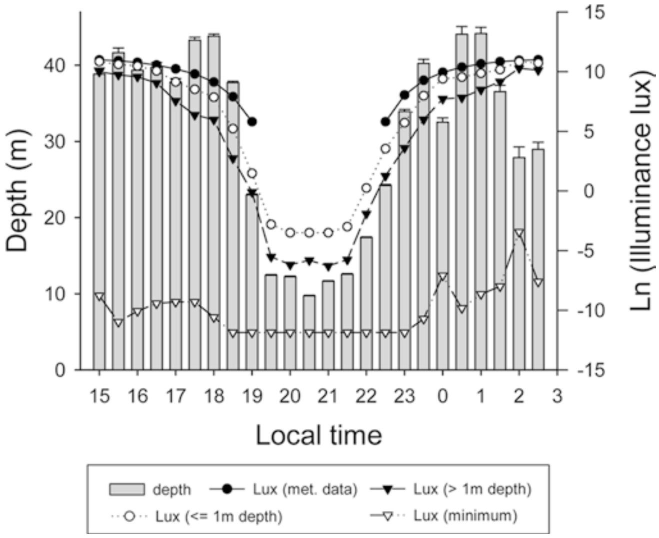


Fig. 4 The mean depth (m) ± SE of fur seals in relation to changes in ln illuminance (lux) (*symbol*) is plotted as the surface illumination averaged across all conditions (see Materials and methods); and from TDLRs at depths ≤ 1 m, at all depths > 1 m and the minimum illuminance recorded each hour

Changes in illumination with depth

The relationship between illuminance and depth was examined by plotting the natural logarithm of the illuminance against depth for each 4-h period. Illumination decreased with depth in each 4-h period (Fig. 5A). Between 0600 and 1400 hours LT the mean ln illuminance showed a relatively linear decrease with depth, with the exception of a decrease within the top 5-m. At 2200–0600 hours LT and 1400–2200 hours LT there was a curve-linear decrease in ln illuminance with depth. However, there was no evidence that this pattern was related to the sensitivity of the TDLR light sensor, as the point at which the curve flattened out occurred at different absolute illuminances (Fig. 5A).

The relationship between transmittance and depth was examined by plotting ln transmittance against depth for each 4-h period. At all times of the day, transmittance decreased rapidly within the top 5-m (Fig. 5B). At 2200–0200 hours LT ln transmittance decreased linearly to 25 m and remained relatively constant at around 60 m and then decreased rapidly at greater depths. Similarly at 0200–0600 hours LT there was a linear decline to 50 m, at 50–80 m ln transmittance was relatively constant but decreased thereafter. Between 0600 and 2200 hours LT ln transmittance decreased linearly down to 120 m, followed by a rapid decrease at greater depths.

Attenuation coefficients were calculated for each 4-h period and for each female (Table 2). Periods where females made less than ten dives were excluded from the analysis (W1206, W1308, W1470 and W2921). The mean attenuation coefficient was 0.140 ± 0.014 m^{-1} and coefficients from all 4-h periods ranged from 0.015 to 0.351 m^{-1}. Attenuation coefficients were more variable at night (2200–0200 hours LT: Table 2). Excluding these night-time values the mean attenuation coefficient was 0.122 ± 0.005 m^{-1} (range 0.068–0.224). There was no difference in the attenuation coefficient measured by Mk5 and Mk6 TDLRs (Wilcoxon two-sample test $z = 1.14$ $P > 0.25$). There was also no difference in the attenuation coefficient between the two Mk6s ($z = 1.24$ $P > 0.22$). Differences in attenuation coefficient between individual females were compared using their 95% confidence intervals (Table 2). Coefficients from W1206 and W1308 were highly variable and the only other difference was W3867, which had a significantly lower attenuation coefficient.

The mean attenuation coefficient for each deployment was negatively correlated with mean dive depth (Spearman rank test $r = -0.64$, $n = 10$, $P < 0.05$) and mean dive duration during each foraging trip ($r = -0.66$, $n = 10$, $P < 0.04$). By excluding the outlier of 0.015 m^{-1} the correlation between attenuation coefficient and depth ($r = -0.76$, $n = 10$, $P < 0.02$) and duration ($r = -0.73$, $n = 10$, $P < 0.02$) was increased. However, the mean attenuation coefficient was not correlated with start date of foraging trip, foraging trip duration, dive frequency or percentage of dives per night ($P > 0.14$ in all cases).

Ship surveys

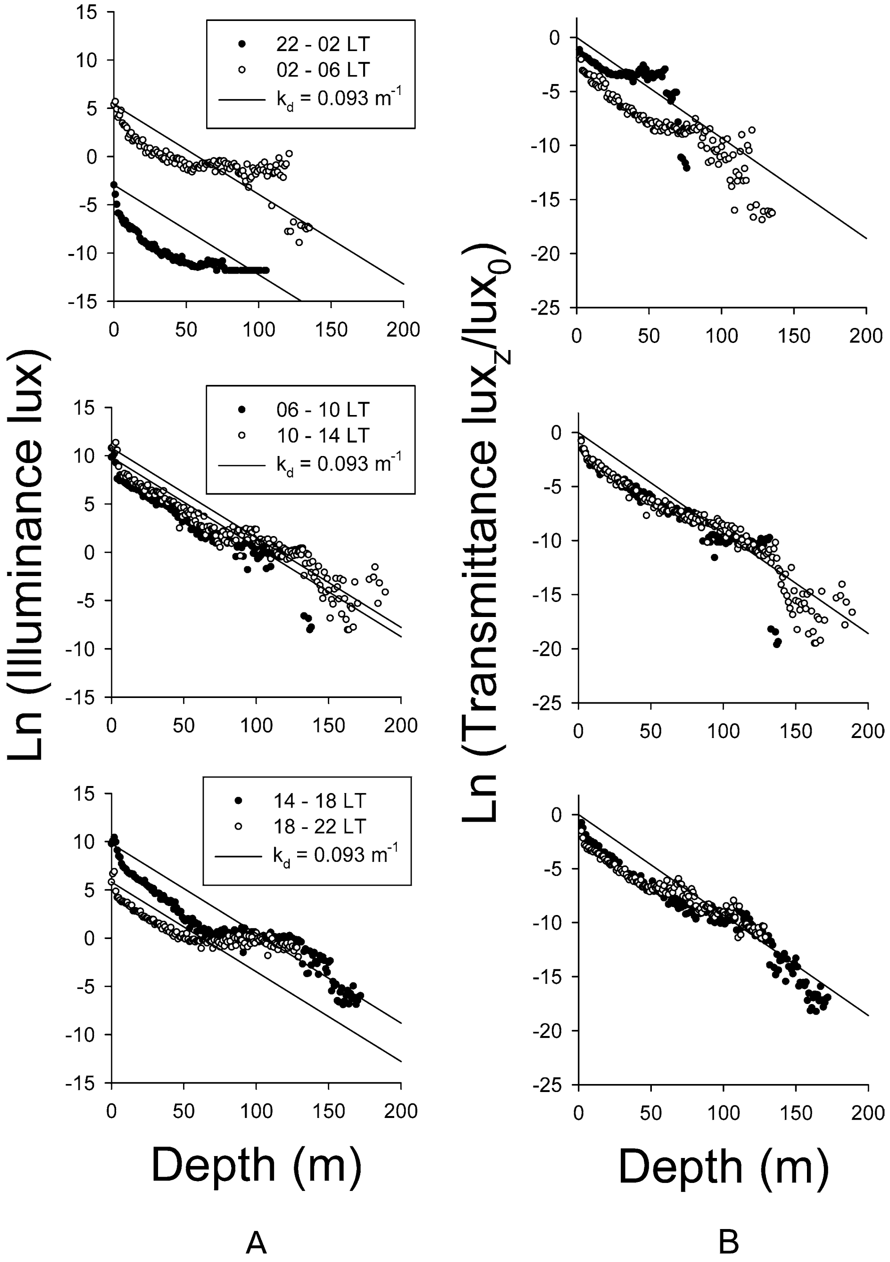
From the ship the relationship between ln illuminance and depth was approximately linear with the exception of measurements taken in the evening (Fig. 6). In these cases there was a linear decrease with depth but at 60–100 m the sensor readings levelled off at around 0.5 lx. The mean attenuation coefficient was 0.093 m^{-1} (SE = 0.005) and values ranged between 0.066 and 0.137 m^{-1} at different locations (Table 3). There was no correlation between the attenuation coefficient and latitude, longitude or hour of day (Spearman rank test $P < 0.18$, in all cases).

Discussion

Calibration

While it was not our specific objective to examine absolute light levels using the TDRs, the output from Mk5 and Mk6 TDLR light sensors was found to show a linear increase with ln illuminance over the range 1 lx–100 klx. The spectral sensitivity of the TDLR did not correspond to the theoretical spectral composition of light at depth or the maximum spectral sensitivity ($\lambda = 500$ nm) of fur seal vision (Lavigne and Ronald 1975). We attempted to overcome the errors associated with this by calibrating the TDLR in light of 400–750 nm which is closer to the spectral composition of light at depth and using a light meter with a spectral sensitivity of 400–700 nm. The extent to which

Fig. 5 **A** The relationship between ln illuminance (lux) and depth (m) and **B** the relationship between ln transmittance and depth recorded by TDLRs for each 4-h period. *Solid lines* show the change in illuminance and transmittance calculated using a mean attenuation coefficient of 0.093 m^{-1} for South Georgia (Table 3)



calibrations may have varied between the different instruments was unknown because the calibration was limited to only one instrument of each TDLR type. However, there was no difference in the mean attenuation coefficient measured by two different Mk6s during deployments, which suggested that any differences in calibration were small. Therefore, even though we cannot be sure the illuminances measured in this study are calibrated accurately, there is evidence to suggest they are internally consistent and broadly indicative of actual illuminance. More recent devices (model Mk9) are now calibrated in W cm^{-2} rather than previous uncalibrated units and may in future provide more accurate measurements of absolute illuminance at depth.

The range in illuminances used in the calibration was likely to be encountered by fur seals at the sea surface around South Georgia in summer (Fig. 4). It was therefore surprising that during deployments illuminances as high as 690 klx were recorded at the sea surface. Wave-focusing of sunlight in the first few centimetres of the water column could account for some increase in surface values but it is possible that the mismatch in readings was due to problems associated with calibration (as discussed above). These readings represented less than 0.4% of all light readings recorded and were therefore unlikely to bias the results.

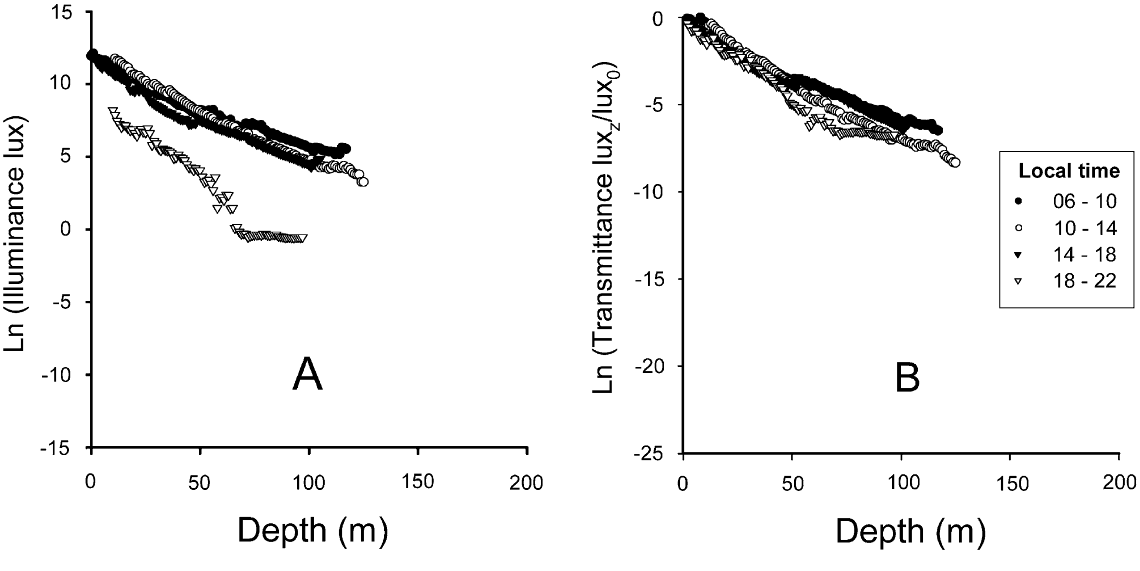
It was not possible to check the calibration of light sensors at illuminances below 1 lx because of the difficulty of measuring low light levels in the laboratory and

Table 2 Attenuation coefficients K_d (m^{-1}) in top 50 m of the water column determined from light measurements made by TDLRs deployed on female Antarctic fur seals. The attenuation coefficient was calculated for 4 h periods (n = number of individuals) and for each individual seal (n = number of 4 h periods). The 95% confidence interval (CI), the range of coefficients of determination (R^2) for each regression line and the significance (P) of the F test are given. All regression lines were highly significant (F test $P < 0.0001$ with the exceptions marked * with an *asterisk* where P values ranged from < 0.0001–0.05)

	n	K_d (m^{-1})	95% CI	R^2
Local time (hours)				
2200–0200	10	0.170	0.095–0.245	0.35–0.95 *
0200–0600	10	0.133	0.104–0.162	0.76–0.93
0600–1000	6	0.113	0.074–0.151	0.67–0.93
1000–1400	8	0.119	0.091–0.147	0.78–0.95
1400–1800	8	0.126	0.100–0.152	0.79–0.99
1800–2200	9	0.113	0.088–0.138	0.80–0.98
Tag number				
W1206	3	0.188	−0.165–0.541	0.88–0.93
W1308	2	0.240	0.037–0.443	0.85–0.91
W1470	5	0.118	0.087–0.148	0.78–0.97
W1765	6	0.095	0.062–0.128	0.83–0.95
W2301	6	0.127	0.086–0.168	0.43–0.98
W2379	6	0.123	0.061–0.185	0.35–0.96
W2921	5	0.154	0.093–0.215	0.75–0.92
W3805	6	0.137	0.104–0.170	0.40–0.90 *
W3821	6	0.155	0.116–0.194	0.58–0.99
W3867	6	0.076	0.050–0.102	0.84–0.94

the accuracy of the light meter used. The relationship between ln illuminance and depth showed that deviations from a linear relationship occurred at different absolute illuminances for different hours of the day (Fig. 5A). Nevertheless, this still showed that the sensors continued to work at low illumination and the decrease in illumination with depth was relatively consistent with the predicted decrease measured by the ship survey at South Georgia. The only period that the TDLR light sensor appeared to lack sufficient sensitivity was during 2200–0200 hours LT when the output was zero at depths greater than 80 m.

Fig. 6 **A** The relationship between ln illuminance (lux) and depth (m) and **B** ln transmittance and depth (m) recorded by ship surveys at South Georgia (Table 3)



Changes in illumination when diving

Fur seals were in conditions ranging from full sunlight to the equivalent of minimum starlight when diving (Lythgoe 1979). During the descent and ascent phases of dives, the light levels changed at a relatively constant rate but at the bottom of dives there were small fluctuations in light associated with changes in depth. In comparison to the change in light with depth, light readings at the surface were highly variable. The rapid frequency of these changes suggested that they were due to the behaviour of the animal rather than changes due to cloud cover. On the surface, fur seals show greater variation in swim speeds than when diving (Boyd et al. 1995). These are thought to include travel between patches of krill (Boyd 1996) as well as grooming bouts (Gentry et al. 1986). In addition, fur seals often "porpoise" while swimming at the surface and all these types of activities could have contributed to the high variation in surface light levels.

Fur seals change their dive depth in response to the vertical migration of krill to the surface at night (Croxall et al. 1985). If fur seals were feeding at a particular light threshold then it would be expected that there would not be a strong diel pattern of light level recorded by TDRs. However, based on the mean illuminance during diving it appeared that the diel pattern of diving was not based on some optimum light level (Fig. 4). This agreed with the hypothesis that the vertical migration pattern of krill is triggered by large changes in light intensity, particularly at dawn and dusk rather than animals seeking some optimal light level (Godlewska 1996).

If fur seals are able to locate their prey visually then it would be predicted that they would be able to locate

Table 3 The attenuation coefficient K_d (m^{-1}) in top 50-m of the water column determined from ship surveys at South Georgia on 18 January and 19 February 1996. The 95% confidence interval (CI) and the range of coefficients of determination (R^2) for each regression line are given. All regression lines were highly significant (F test $P < 0.0001$)

Location	Hours (local time)	K_d (m^{-1})	95% CI	R^2
18 January 1996				
53.8° S 37.6 W	08:00	0.088	0.086–0.090	0.99
53.6° S 37.7 W	09:00	0.091	0.088–0.096	0.98
53.4° S 37.7 W	10:00	0.067	0.062–0.072	0.95
53.3° S 37.8 W	11:00	0.097	0.093–0.101	0.98
53.2° S 37.8 W	12:00	0.091	0.085–0.097	0.97
53.2° S 37.9 W	13:00	0.087	0.082–0.092	0.97
53.4° S 37.9 W	14:00	0.080	0.074–0.087	0.94
53.5° S 37.8 W	15:00	0.066	0.062–0.070	0.97
53.7° S 37.8 W	16:00	0.102	0.098–0.106	0.98
53.8° S 37.7 W	17:00	0.121	0.113–0.129	0.96
19 February 1996				
53.4° S 38.3 W	18:00	0.105	0.101–0.108	0.98
53.4° S 38.5 W	19:00	0.094	0.091–0.097	0.99
53.3° S 38.7 W	20:00	0.078	0.068–0.088	0.85
53.2° S 38.8 W	21:00	0.137	0.119–0.155	0.91

prey more easily on nights of full moon. There were too few deployments in this study to test this hypothesis, however Galapagos fur seals (*Arctocephalus galapagoensis*) increased their dive depth at higher lunar intensities, in response to changes in the vertical migration of myctophid fish (Horning and Trillmich 1999). Although it is not known if krill show this pattern, myctophids are also taken by Antarctic fur seals (Reid and Arnould 1996) and the response of Antarctic fur seals could therefore be similar to that of Galapagos fur seals.

Fur seals may be using different sensory mechanisms to catch prey at low light intensities. Blind but well-nourished seals have been observed in the wild (Newby 1970) showing that seals can orientate and hunt successfully without vision. Harbour seals (*Phoca vitulina*) can use their whiskers to detect water velocities associated with fish movement (Dehnhardt et al. 1998; 2001) and therefore Antarctic fur seals may forage in a similar way.

Optical properties of water

Illuminance measured by TDLRs did not show a simple pattern of attenuation as reported for clear oceanic water (Lalli and Parsons 1993). At all times of the day there was stronger attenuation in the top 50 m. The broad spectral sensitivity of the photodiode in TDLRs may have accounted for the rapid decrease of illuminance with depth due to absorption of infra-red and red wavelengths of light in the surface waters. Previous measurements in Antarctic waters have shown that areas lacking phytoplankton blooms have linear attenuation curves, but with blooms attenuation was greatest in the top 25 m followed by less attenuation at greater depths (Mitchell and Holm-Hansen 1991b). The attenuation coefficient for PAR in the mixed layer is well correlated with pigment concentration (Smith and Baker 1978a; 1978b; Mitchell and Holm-Hansen 1991b).

Attenuation coefficients measured by TDLRs ranged from 0.015 to 0.351 m^{-1}. The lowest value was considerably smaller than reported values for clear oceanic water (Table 4). Most values were in the range recorded by the ship survey in the region of the shelf break to the northwest of Bird Island where fur seals are known to forage (Boyd et al. 1998). Overall, the mean attenuation coefficient from TDLRs was in the upper range of values for oceanic waters (Table 4). When fur seals made shorter and shallower dives TDLRs also recorded greater light attenuation coefficients, as seen by the negative correlation between mean attenuation coefficient and mean dive depth for each deployment. In addition, the variance in attenuation was greater at night than during the day—perhaps evidence of more biomass in surface layers at night. These findings suggested that Antarctic fur seals were tending to dive in turbid waters

Table 4 Attenuation coefficients (K_d m^{-1}) for wavelengths 535 and 550 nm for Antarctic waters and for water types I–III (Jerlov 1976) in comparison to measurements (400–700 and 350–1,100 nm) in this study

λ (nm)	K_d (m^{-1})	Location / Water type	Reference
552	0.075–0.131	South Georgia	Fenton et al. (1994)
552	0.114–0.131	South Georgia (NW locations)	Fenton et al. (1994)
552	0.098–0.151	Bransfield Strait	Fenton et al. (1994)
552	0.070–0.172	Various Pacific and coastal waters	Fenton et al. (1994)
535	0.069–0.172	South Shetland Islands and Drake Passage	Stramski and Montwill (1982)
550	0.063	Type I (Sargasso Sea)	Jerlov (1976)
550	0.089	Type II	Jerlov (1976)
550	0.122	Type III	Jerlov (1976)
400–700	0.066–0.137	South Georgia (ship survey)	This study
350–1,100	0.015–0.351	South Georgia (fur seals)	This study

containing large amounts of light attenuating particles such as phytoplankton and/or dense aggregations of krill.

Conclusions

This study showed that TDLRs have the potential to measure the relative change in illuminance with depth when fur seals are foraging. With additional calibration and appropriate selection of detector they may also be capable of measuring the absolute illuminance. We showed that female fur seals do not change the diel depth of foraging to feed in regions of constant illuminance and we also showed that diving occurs in regions where there is relatively high turbidity in the water column, probably as a result of krill.

Future studies would be improved by developing instruments with photodiodes that were most sensitive to the spectral variation in underwater light rather than the broadband sensor currently used. This would allow a separation of artefactual changes in irradiance readings due to rapid reduction in red and infrared wavelengths within the first few metres of the water column from changes in either the position of the sensor with regard to down-welling light (due to orientation of the animal) or increased attenuation due to the bio-optical properties of the water. This will be crucial in developing the use of these instruments for studies of vision and productivity of waters in which marine mammals feed.

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