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The tide as zeitgeber for Weddell seals

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Abstract The haul-out and underwater activity patterns of five Weddell seals were investigated in relation to the tide. Electronic recorders measured the seals' dive depth and internal body temperature simultaneously. Diving and temperature data were analysed with the help of time series analyses tools. We identified a half-day (semicircadian) rhythm in underwater activity and body temperature. A close correlation was found between the rhythmicity of the tide and the timing of the seals' underwater activity and oscillations of their body temperature. We propose that the tide is the principal zeitgeber for the Weddell seals' ultradian cycle of behaviour during the austral summer.

Introduction

The day-night rhythm is one of the most prominent of all biological rhythms. Whenever the conditions of their environment are devoid of zeitgeber cues, mammals show free-running endogenous circadian rhythms. However, these constant conditions are rarely found in nature. An exception are polar regions where the most important zeitgeber of temperate latitudes, the light-dark cycle, is weak or absent during the continuous daylight of the polar summer. Nevertheless, some antarctic pinnipeds show a diel and, therefore, predictable haul-out behaviour (Gilbert and Erickson 1977) during summer, which allows their haul-out peak to be used for

census surveys, even though a series of physical and biological factors lead to variations in the diel haul-out behaviour (Thomas and DeMaster 1983). In particular, this has been reported for the Weddell seal (*Leptonychotes weddellii*). Previous studies on the activity patterns of Weddell seals in fast-ice areas (e.g. Müller-Schwarze 1965; Smith 1965; Siniff et al. 1971; Kaufman et al. 1975; Thomas and DeMaster 1983; Reijnders et al. 1990) and pack-ice areas (e.g. Stirling 1969; Siniff et al. 1970; Gilbert and Erickson 1977) indicate that Weddell seals exhibit a diurnal haul-out pattern that varies seasonally and geographically. Although haul-out behaviour appears to be driven by a circadian rhythm based on the diurnal change in solar radiation, no diurnal patterns could be detected in the secretion of the hormones melatonin (Griffiths et al. 1986) or cortisol (Barrell and Montgomery 1988) in Weddell seals during the austral summer.

From January to March, the present study period, numbers of Weddell seals hauled out on the ice peak at around noon; only a small number of seals were visible during midnight hours when they prefer to dive, presumably to feed. The overall impression obtained from most field and aerial observations is that weather has a strong influence on the number of Weddell seals present on the ice. For example, a negative correlation was found between seal numbers observed and wind velocity (Smith 1965; Gilbert and Erickson 1977) while there was a positive correlation between seal number and intensity of solar radiation (Müller-Schwarze 1965; Smith 1965). In contrast, Siniff et al. (1970) monitored the activity patterns of female Weddell seals instrumented with radio transmitters and found that air temperature, wind velocity and wind chill showed little effect on seal activity except for "severe weather", but also on "good days" animals wandered into the water during their peak haul-out period for no observable reason. Interestingly, none of the studies mentioned above considered the effect the tide might have on the haul-out and foraging behaviour of seals. During our studies on Weddell seals in the eastern Weddell Sea we observed strong tidal

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action with amplitudes of about 2 m, detectable by the yellowish band of ice algae at the ice shelf edge during low tide. As the Weddell seal spends most of its life foraging at sea, we propose that its diurnal behaviour patterns are synchronised with the oscillations of a zeitgeber that affects the seal's marine environment and, in particular, the seal's prey. Therefore, we investigated the activity behaviour of individual Weddell seals in relation to the tide during austral summer.

Materials and methods

Weddell seals were studied at Drescher-Inlet ($72^{\circ}52'S$ $19^{\circ}26'W$), eastern Weddell Sea, from mid-January to end of February 1995. Solar elevations were 36.6° at 12 noon and 2.6° at midnight at the beginning of our study (23 January). The decrease in solar elevation amounted to 8.4° during the course of our study (23 Jan/20 Feb), corresponding to 28.2° (noon) and -5.8° (midnight). We started our investigation during a period of continuous daylight and ended with only a few hours per day of complete darkness. Therefore, we define a day as the 12-h period with highest solar elevations (6 a.m.–6 p.m.) and night as the 12-h period with lowest solar elevations (6 p.m.–6 a.m.). The time at Drescher Inlet is UTC minus a mean of 76 min. However, all logger times were set to local noon (1200 hours UTC minus 60 min). Times were set without regard to the time equation.

Electronic instruments and data processing

Five adult Weddell seals (two females, three males) were immobilised (see below) and then equipped with one-channel data-loggers (Pillboxlogger, 8 bit, Driesen and Kern, Bad Bramstedt, Germany). Each seal had two logger units, one fitted with pressure (0–80 bar) and the other with temperature sensors ($+10$ to $+40^{\circ}C$) to measure dive depth and internal body temperature simultaneously. The storage capacity allowed 130,000 recordings. Triggered at 8-s measuring intervals data could be recorded continuously for a maximum of 12 days. The logger housing, a titanium tube, measured 12 cm in length and 1.8 cm in diameter. Seawater intake or condensation inside the housing was prevented by filling the titanium tubes with an inert liquid (3 M Fluorinert TM Dielektrika FC-77, Neuss, Germany). An added advantage of this procedure was that it made further strengthening of the tube wall against hydrostatic pressure unnecessary. The dive-depth logger was fixed by two house clamps on a gauze mat of 5×10 cm and then glued onto the seal's dorsal hair using quick-setting epoxy resin. Body temperature was measured in the seal's stomach. The logger was gently introduced via a stomach tube and after recapture of the seals retrieved by means of an endoscope (CF 10L Coloscope, Olympus, Hamburg, Germany) of flexible length of 175 cm and a foreign-body retrieval forceps (FG-15 U, Olympus). The instruments were then removed and the raw data retrieved from the logging units. The computer program "Multidat" (Mohr 1988) was used to analyse rhythmic components in temperature and underwater activity data as actograms, Fourier analyses, chi-square periodograms and cosinor fits. Actograms are shown in the form of double plots. This allows the recognition of a possible phase shift in the data, particularly when the (free-running) circadian rhythm extends over the midnight time mark. Bars represent diving activity or temperature deviations from mean body temperature (see Fig. 1 for further explanation).

The Fourier analysis reveals a spectrum of intensities of basic harmonic wavelengths. Dividing a time series into n periods of same duration (e.g. five 24-h periods) and Fourier-transforming these periods leads to 5 Fourier spectra. Simple summing of these spectra

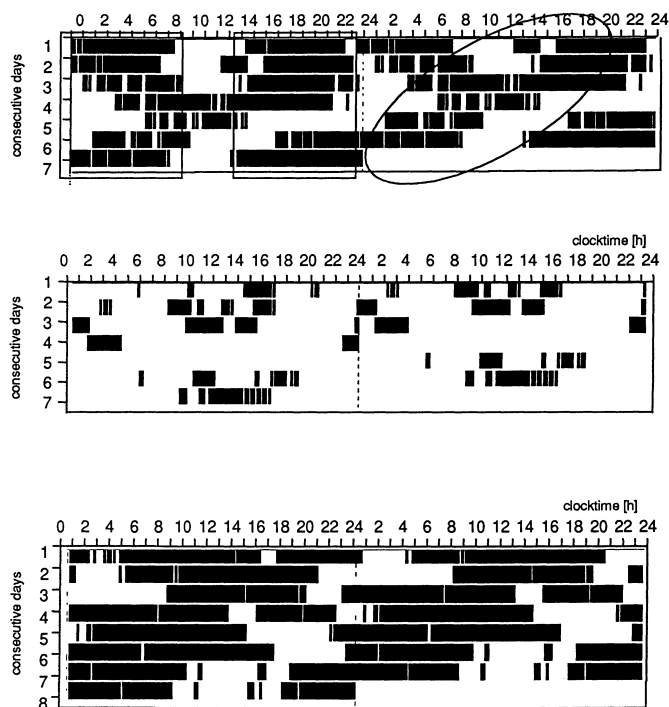


Fig. 1a–c Actograms of seal 4 and 1 (seal 4 diving activity (a), body temperature (b), seal 1 diving activity (c) of 7 (seal 4) and 8 (seal 1) consecutive days. Each day appears below the previous on the *ordinates*. The *abscissa* consists of two 24-h cycles, where the second 24-h period represents the consecutive day. This consecutive day appears again in the next line and begins the next double 24-h period. Consequently there is the loss of 1 day at the end of the *right hand pane*. The *solid bars* represents periods of diving activity (values ≥ 12 m) and (c) or values 20% above the average body temperature (b) respectively. The *squares* mark areas that represent the semicircadian activity pattern, whereas the *ellipse* marks the free-running circadian rhythm

to obtain information on the mean intensity may result in misinterpretation, because it is possible that a harmonic oscillation has a high intensity in the different periods, but not necessarily the same phase angle. Therefore, the intensities are calculated using the single sine- and cosine-components of the harmonics that give evidence of the phase. The separate sums of the sine- and cosine-components of all the spectra will conserve the underlying time structure, so that only those harmonic oscillations with the same phase angle of the sine- and cosine-component in all periods investigated will show a distinct intensity (phase-corrected Fourier analysis).

To obtain chi-square periodograms, the time series has to be divided into equidistant periods as for the Fourier analyses. In contrast to the Fourier analyses, however, the chi-square periodograms are not dependent on the assumption that the oscillations are harmonic. Evaluation of the variance of mean values inside the equidistant periods leads to identification of periodically recurring events. This method leads to the more precise detection of significant rhythms.

A cosinor curve fit means that a set of cosine waves with different wavelengths is fitted to the data. Using this technique, the correlation coefficients of the fitted cosine waves with the original data, their amplitudes and their acrophases will be obtained. The acrophase represents the time at which the rhythm attains its maximum. All techniques are described in detail in Nelson et al. (1979), Monk (1982), Mohr and Krzywaneck (1988), and Mohr (1994). The harmonic constants of the tide (Krause and Catewicz 1992) were calculated from an annual time series of bottom pressure using the manual and computer program of Foreman (1978). Bottom pressure was measured by an Aanderaa WRL-5 recorder.

Immobilisation

Our former technique of narcosis (Bornemann and Plötz 1993) was modified as follows. Instead of catching the seals in a bag and injecting by hand, we used Telinject blowpipe darts to administer the narcotic drugs from a distance chosen to minimise the seals' defence and flight responses. Thus, undue stress to the animals is prevented and the risk of adverse reactions to the immobilisation is greatly reduced. Moreover, the proportion of the drugs ketamine and xylazine was changed slightly, increasing xylazine and reducing ketamine doses. This not only reduced the total volume administered, but also enabled us to give the ketamine-xylazine mixture as a single shot, and provided greater scope to maintain immobilisation with follow-up doses of ketamine. Thus the protocol for immobilise seals consisted of an initial dose of a mixture of ketamine, xylazine and hyaluronidase described as "Hellabrunner Mischung" (Wiesner 1982) of 4.5 ml/seal (500 mg xylazine + 400 mg ketamine + 150 I.U. hyaluronidase), followed immediately by a shot of 4 ml diazepam (20 mg/seal). With this medication an immobilisation lasting for approximately 45–60 min was obtained in all seals. Immobilisation could be maintained as needed by a small follow-up dose of ketamine (200–300 mg/seal) without any need of intubation to prevent asphyxia. The immobilisation was reversed by administration of the antidote yohimbine. To minimise the effect of narcosis on the rhythmic behaviour of the seals, we did not consider the first 24 h of the received data sets.

Results

Diving and haul-out patterns, as well as concurrently recorded body temperature data, were obtained for periods of 11 days (seal 1, 23 Jan to 03 Feb), 8 days (seal 2, 30 Jan to 07 Feb), 4 days (seal 3, 08 Feb to 13 Feb), 7 days (seal 4, 08 Feb to 17 Feb), and 5 days (seal 5, 14 Feb to 20 Feb). Tables 1–3 give the relationships be-

tween the periods of underwater activity and haul-out of the five animals. During the recording period of 29 days, there was a synchronous data overlap of 5 days for seals 1 and 2, of 6 days for seals 3 and 4, and of 4 days for seals 4 and 5. Periods with data overlap were denoted as overlap phase 1–3. We hypothesised that there would be no significant difference between seals within overlap phases with respect to timing or duration of underwater activity and haul-out of the seals. This hypothesis was confirmed using the Mann-Whitney rank sum test ($\alpha = 0.05$), with P -values ranging from 0.1358 to 0.8413.

For all five seals studied, the median start time (Table 4) of underwater activity phases occurred generally at the beginning of the night (as defined under Materials and methods), and the median start time of haul-out phases generally occurred during the day. However, the data of each individual seal were heterogeneous with respect to this day/night pattern. After pooling and distributing the data into 3-h classes, the modal start time of the underwater activity was 7.29 p.m. The four classes between 6 p.m. and 6 a.m. composed 67.3% ($n = 37$) of all start times. The modal start time of the haul-out period was 10.43 a.m., and the four classes between 6 a.m. and 6 p.m. covered 74.5% ($n = 41$) of all start times of haul-out periods. Therefore, about 33% of all underwater activity periods occurred during the day and about 25% of all haul-out periods during the night.

Actograms

Figure 1a gives an example of an underwater activity plot of seal 4 in the form of an actogram. The solid bars

Table 1 Total duration of the underwater activity and haul-out periods of five adult Weddell seals, Feb. 1995, Antarctic (*F* female, *M* male)

Seal	Weight (kg)	Sex	Total data set (h)	Periods (<i>n</i>)	Activity time (h)	Haul-out time (h)	Activity time (%)	Haul-out time (%)
1	314	F	265.29	13	165.60	99.69	62.42	37.58
2	272	M	193.18	10	138.51	54.67	71.70	28.30
3	250	M	132.70	7	70.35	62.35	53.01	46.99
4	318	F	185.33	13	133.22	52.31	71.88	28.12
5	249	M	145.53	7	110.78	34.77	76.11	23.89

Table 2 Average duration (h) of the underwater activity periods of five adult Weddell seals, Feb. 1995, Antarctic (V coefficient of variation)

Seal	Mean	SD	SE	Max	Min	Median	V
1	12.74	5.07	1.41	19.02	4.62	14.66	0.40
2	13.85	5.23	1.66	23.42	6.54	14.30	0.38
3	10.05	11.63	4.40	34.56	2.76	4.53	1.16
4	10.25	4.43	1.23	19.34	2.73	8.46	0.43
5	15.83	6.19	2.39	25.93	9.60	17.35	0.39

Table 3 Average duration (h) of the haul-out periods of five adult Weddell seals, Feb. 1995, Antarctic (V coefficient of variation)

Seal	Mean	SD	SE	Max	Min	Median	V
1	7.67	5.07	1.41	15.72	1.29	6.74	0.65
2	5.47	3.29	1.04	11.23	1.42	4.70	0.60
3	8.91	4.12	1.56	14.51	2.73	10.13	0.46
4	4.02	2.97	0.82	11.24	0.86	4.27	0.74
5	4.97	3.95	1.49	10.24	1.03	4.27	0.80

Table 4 Median start time of the underwater activity and haul-out periods of five adult Weddell seals, Feb. 1995, Antarctic

Seal	Underwater activity (local time)			Haul-out (local time)		
	Median	Min	Max	Median	Min	Max
1	07:00 p.m.	00:00 a.m.	10:00 p.m.	11:00 a.m.	06:00 a.m.	11:00 p.m.
2	05:00 p.m.	00:00 a.m.	11:00 p.m.	04:30 p.m.	01:00 a.m.	11:00 p.m.
3	08:00 p.m.	04:00 a.m.	11:00 p.m.	09:00 a.m.	01:00 a.m.	02:00 p.m.
4	12:30 p.m.	00:00 a.m.	07:00 p.m.	10:00 a.m.	00:00 a.m.	11:00 p.m.
5	04:30 p.m.	01:00 a.m.	10:00 p.m.	09:00 a.m.	00:00 a.m.	12:00 p.m.

represent periods of underwater activity (depths ≥ 12 m) during 7 consecutive days. The open areas represent periods of rest. Figure 1b shows the actogram of the simultaneously recorded data on body temperature of seal 4. Solid bars represent periods in which the body temperature exceeds its mean value (36.7°C) by 20%. The solid activity bars of Fig. 1a correspond approximately with the open areas in Fig. 1b indicating a negative correlation between underwater activity (dive depth) and body temperature. Moreover, Fig. 1a shows two blocks of underwater activity (squares). The blocks include the early morning and early evening hours and indicate that there are two phases each of activity (low temperature values) and rest (high temperature values) per day. Although a slight offset can occur (e.g. 14 h), both activity and temperature data support the presence of a 12-h rhythm. The ellipse marks an additional band of activity. The beginning of the first solid bar in each day causes a slope in the band and ellipse. This free-running circadian periodicity underlies the 12-h ultradian, or semicircadian, period. However, the actograms of the seals studied were not homogeneous in this respect. In some actograms only one component (e.g. 24 h in Fig. 1c) is clearly discernible. To decide whether the semicircadian rhythm is masked by the circadian rhythm or vice versa, we characterised the basic body temperature and diving activity rhythms using time series analyses tools.

Fourier analyses, chi-square periodograms and cosinor fits

The Fourier analyses generally showed that significant oscillations with periods of 24 and 12 h (Table 5) exist in both diving activity patterns and in body temperature profiles. The circadian oscillations ranged widely from 19.9 to 25.1 h and showed a narrow range between 11.2 and 12.0 h for the 12-h oscillation. However, when analysed with consideration of the phase, all dive and temperature profiles only revealed the 12-h oscillation with significant intensity ($P < 0.05$), with the exception of the dive profile of seal 1. A comprehensive diagram of the several frequencies representing the time course of diving activity and body temperature of all seals is given in Fig. 2. As can be seen from this diagram, the semicircadian rhythm was predominant in our data. These 12-h oscillations were then analysed using chi-square periodograms. The results of the chi-

Table 5 Intensities of wave length (λ) of semicircadian (12 h) and circadian (24 h) oscillations (based on Fourier analyses) in diving activity and body temperature of five adult Weddell seals, Feb. 1995, Antarctic [(-) no significant intensity]

Seal	Diving activity		Body temperature	
	$\lambda_{12\text{ h}}$	$\lambda_{24\text{ h}}$	$\lambda_{12\text{ h}}$	$\lambda_{24\text{ h}}$
1	(-)	24.0	12.0	(-)
2	(-)	24.0	(-)	21.3
3	(-)	25.1	(-)	(-)
4	11.9	19.9	11.9	19.9
5	11.3	22.6	11.2	(-)

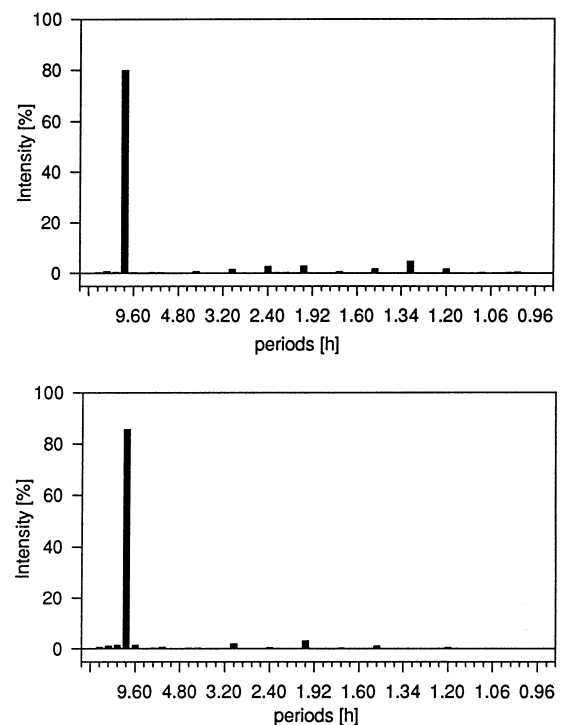


Fig. 2 Averaged power density spectrum of the several periods (h) which form the time course of diving activity (*above*, seals 2, 3, 4, 5) and body temperature (*below*, seals 1, 2, 3, 4, 5). Seal 1 was excluded from the diving activity plot as the analyses of its data only showed the 24-h component. The *y*-axis is graduated in percentages (of all intensities). The dominant *bar* in each spectrum represents the 12-h cycle

square analyses are given in Table 6. The Fourier analyses of the diving pattern and body temperature profile show distinct intensities of 24-h and 12-h

Table 6 Comparison of wave length (λ , based on chi-square analyses) and acrophase (*Phase*, based on cosinor fits) of the semi-circadian oscillations in diving activity and body temperature of five adult Weddell seals, Feb. 1995, Antarctic [(–) no significant intensity]

Seal	Diving activity		Body temperature	
	λ (h)	Phase (°)	λ (h)	Phase (°)
1	13.0	143	13.5	83
2	(–)	148 ^a	12.0	130
3	13.0	56	13.0	29
4	12.0	174	12.5	63
5	11.5	127	12.0	72

^a Only for 24-h oscillation

periods. After separately totalling the sine- and cosine-components (phase-corrected Fourier spectra and chi-square periodograms), only the 12-h period remained. It can be concluded that the 24-h rhythm in the raw data was due to a masking effect, which explains why the 24-h period dropped below significant intensity in the analyses (Fig. 2). To determine when the rhythm occurs relative to local time, we calculated the acrophase. The acrophase represents the time at which the rhythm attains its maximum. The acrophases are given in Table 6.

On average the acrophase of diving activity was $125.5^\circ \pm 49.9$ ($\bar{x} \pm SD$) corresponding to 4.11 a.m./p.m. ± 100 min, and those of the body temperature $62.2^\circ \pm 23.6$ ($\bar{x} \pm SD$) corresponding to 2.04 a.m./p.m. ± 47 min. Moreover, the phase relation between the acrophases of diving activity and body temperature was constant, amounting to 63.3° corresponding to 2.07 h (paired *t*-test, $P = 0.0360$).

The tide

Figure 3 shows the tidal curve for the region of Drescher Inlet. The mixed type of tide with a pronounced fortnightly inequality is governed by the semi-diurnal constituents M_2 (principal lunar component, 12.4 h, 41 cm) and S_2 (principal solar component, 12.0 h, 30 cm), and by the diurnal harmonics K_1 (luni-solar diurnal component, 23.9 h, 27 cm) and O_1 (principal lunar diurnal component, 25.8 h, 29 cm). This is characteristic for the southern part of the Weddell Sea (Schwidorski 1997).

To test the performance of the Fourier analyses described above, the 29-day tide record was analysed to result in periods of 11.7 h (S_2), 12.4 h (M_2), 23.4 (K_1) and 25.4 (O_1). Given the limited recording period, these results are acceptable. The Fourier analyses of the tide data (Fig. 4) revealed periods of 11.7 and 12.4 h and two diurnal constituents. The acrophase of the tide as a result of the two tide waves was 113° corresponding to 3.46 a.m./p.m. Figure 5 gives the position of the acrophases of body temperature and diving activity in relation to the acrophase of the tide.

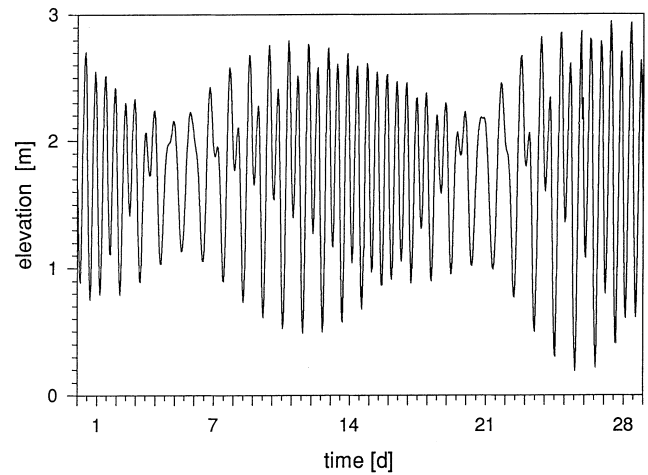


Fig. 3 A 29-day record of tidal heights at Drescher Inlet ($72^\circ 52'S$ $19^\circ 26'W$) during the investigation period (23 Jan to 20 Feb). This type of tide is typical of the southern Weddell Sea

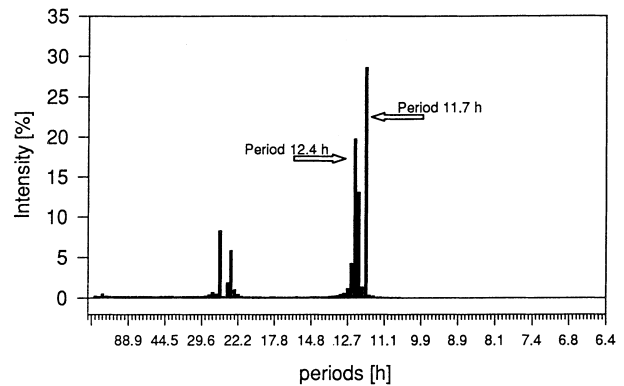


Fig. 4 Power density spectrum of the several periods (h) which form the time course of the tidal movements at Drescher Inlet ($72^\circ 52'S$ $19^\circ 26'W$), Antarctica. The *y*-axis is graduated in percentages (of all intensities). The *x*-axis represents the several periods (h) over the whole investigation period. Next to the 11.7-h period and 12.4-h period the 25-h, 4-h and 23.4-h periods are also discernible

Discussion

Weddell seals occur in largest concentrations on thick stable sea ice (fast ice) attached to the coastal ice shelf barrier. Suitable haul-out sites are available where tidal action and wind form cracks large enough to be used as exit holes. In the study of the diurnal haul-out cycle of Weddell seals, field researchers usually take into account a variety of environmental variables such as solar radiation, cloud cover, air temperature, wind velocity, wind chill, snow drift and the gradual break-up of fast ice during the austral summer. In addition to these physical factors, biological events such as pupping, mating, moulting and the availability of nearby food resources are generally presumed to affect the number of seals hauled out at a certain time of the day.

The diurnal rhythm of Weddell seals has been studied by counting groups of animals (e.g. Müller-Schwarze

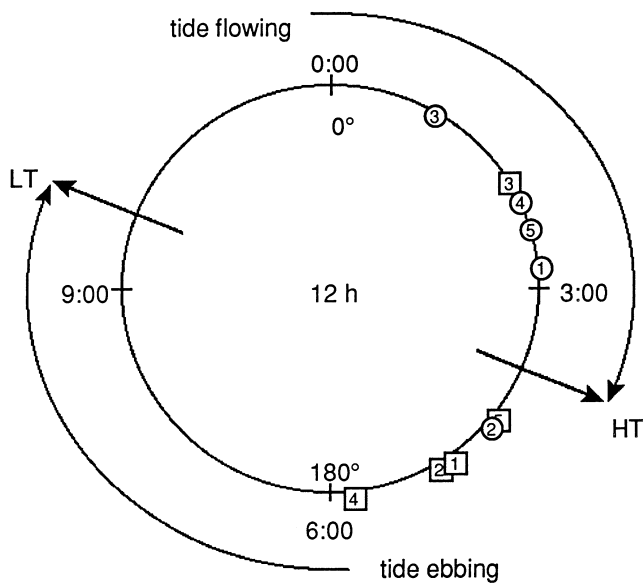


Fig. 5 Cosinor display of the acrophases of diving activity (□) and body temperature (○) of all seals for the 12-h ultradian rhythm. For seal 1 a 24-h rhythm has to be taken into account. The seal's individual acrophases are marked by number (1–5). The acrophase of the tide is marked with an arrow for the high tide (HT) as well as the corresponding low tide (LT). The acrophases can be read either in degree or time

1965; Smith 1965; Stirling 1969; Gilbert and Erickson 1977) and by observing the behaviour of individual seals (e.g. Siniff et al. 1971; Thomas and DeMaster 1983; Reijnders et al. 1990). In general, these studies show that in spring and summer the seals were most active during the night and least active during the day with peak numbers of animals resting on the ice from about mid-day to late afternoon. The diel haul-out patterns may differ considerably among individuals because an unknown proportion of seals is still active under the ice even during daylight. More recently, new information about the migratory and diving behaviour of Weddell seals has been obtained using satellite-linked time depth recorders (Bengtson et al. 1993; Testa 1994). Uncertainties about the magnitude of individual, seasonal and geographic variations in haul-out behaviour complicate obtaining census data for an accurate assessment of seal abundance and distribution, as pointed out in the Antarctic Pack Ice Seals Program coordinated by the SCAR Group of Specialists on Seals (APIS 1995). The underlying assumption in census surveys is that activity patterns follow a diurnal (24-h) cycle. However, if haul-out behaviour followed an ultradian cycle, a substantial error would be introduced if the ultradian cycle is out of phase relative to the assumed diurnal cycle.

The data presented here on the diel underwater activity patterns of Weddell seals at Drescher Inlet confirm the observations made by earlier investigators in principle. However, we found, that 25.5% of all haul-out periods ($n = 55$) occurred during night between 6 p.m. and 6 a.m. Assuming a circadian rhythm for the Weddell seal as proposed by Müller-Schwarze (1965) and Siniff et al.

(1971), the sum of haul-out and underwater activity hours should amount to a value of ca. 24 h per day or approximately to an even multiple of 24 h for a couple of days. However, in the present study we found an uneven multiple of 24 h, i.e. a range of 12.7–21.4 h of rest plus activity time per day (Tables 2, 3, sum of the medians). This clearly indicates that the diurnal cycle of a Weddell seal is shorter than 24 h, at least during austral summer. The amplitudes of circadian rhythms inside our data were much below the level of significance in the chi-square periodograms, which were dominated by a half-day (semicircadian) rhythm (Table 6). While the chi-square analysis showed significant oscillations only with periods ranging between 11.5 and 13.5 h, the Fourier analysis nevertheless indicates that a basic circadian rhythm does exist. This 24-h rhythm had a very low amplitude in both the seals' body temperature and diving activity, and the wide range of 19.9–25.1 h (Table 5) indicates that these parameters follow free-running rhythms during the continuous daylight of the austral summer.

The 24 h rhythm in body temperature is known to be the most stable of all physiological rhythms in mammals other than seals. The very low level of circadian rhythmicity in the body temperature of Weddell seals is, however, consistent with the absence of a circadian pattern in the secretion of melatonin (Griffiths et al. 1986) or melatonin and cortisol (Barrell and Montgomery 1988). A low-amplitude rhythm of plasma melatonin has been found in Adélie penguins but could only be demonstrated in a small number of birds (Cockrem 1990). A circadian rhythm in locomotion (Müller-Schwarze 1968) and body temperature (e.g. Cockrem 1990) was also found in Adélie penguins. The fact that similar haul-out and underwater activity patterns in the overlap phases 1–3, as well as the pronounced 12-h rhythms, were found in the seals studied indicates that the same zeitgeber is responsible for the seals' behaviour. The range of 11.5–13.5 h inside the diving activity and temperature data is consistent with the two tidal constituents S_2 and M_2 presented in Figs. 3 and 4. We propose that the tide is the principal zeitgeber of the seals' ultradian (semicircadian) rhythm of behaviour. The effect of tides (e.g. Paton 1979; Pauli and Terhune 1987; Yochem et al. 1987) or lunar cycles (e.g. Watts 1993) on the haul-out behaviour has been well documented in some other seal species but not yet in the Weddell seal. Siniff et al. (1971) found that environmental variables had a significant influence on Weddell seal behaviour only between 5 p.m. and 9 p.m.; the reason for this was not clear. The Fourier analyses in the present study yielded a significant relation between the acrophases of body temperature and diving, with an activity peak (seals 1, 2, 4, 5) between 4 p.m. and 6 p.m.; at this time the tide is ebbing. The peak of body temperature precedes the underwater activity peak (Fig. 5). Seal 3 did not fit the relationship mentioned above very well: the average duration of underwater activity and haul-out periods deviated from those of the others. Since the data set of seal 3 was the shortest (4 days), we cannot

exclude the possibility that this is an artefact due to the comparatively short data record (Tables 1–3) and might not have been found in a long-term record.

The body temperature of Weddell seals, measured as aortic blood temperature, drops during prolonged dives (Kooyman et al. 1980) or just before diving (Hill et al. 1987). The reduction in body temperature suggests that the Weddell seal may be decreasing the metabolic rate of its central organs to reduce O₂ consumption and extend its diving capacity (Hill et al. 1987). In contrast, locomotory muscle temperature is not affected by diving activity (Ponganis et al. 1993). Since we measured body temperature in the seal's stomach, a temperature decrease could be caused by the ingestion of fish or other cold prey as described for seabirds in Wilson et al. (1992). In our study, only 1.1% of the total activity period of all seals (618 h) showed temperature drops that had been described as precipitous drop with exponential rise (PDER) events which are associated with food intake (Wilson et al. 1992). In addition, the median duration of the PDER events was 38.2 min (MIN = 20.5 MAX = 131.2), which is much below the described semicircadian wavelength of about 12 h. The median wet mass of fish species taken by Weddell seals in the area of Drescher Inlet ranged between 15 and 173 g (Plötz et al. 1991) while the wet mass of fishes used to measure food intake by stomach temperature sensors in harp seals (Hedd et al. 1996) was considerably larger (514–7591 g). Although it is conceivable that food intake is a cue in the seals' diurnal cycle, the fish taken in the region of the study site are in general too small to cause a PDER event. The number and duration of temperature drops in the present study are too small to cause the observed 12-h rhythmicity in temperature behaviour and thus were negligible. Of course, a steady intake of a relatively large number of food items, too small to cause apparent PDER events, could depress stomach temperature during diving as well. If this occurs regularly it would cause a temperature rhythm similar to the diving activity. However, Handrich et al. (1997) pointed out that in king penguins a metabolic regulation in the form of a slower metabolism of cooler tissues resulting from physiological adjustments is associated with diving *per se*. As a consequence, we assume that food intake has only minor influence on the stomach temperature rhythm, which is more likely to be affected by blood temperature.

There is a great deal of evidence that the foraging behaviour of seals is related to both behaviour and abundance of their prey. Boyd and Arnborn (1991) proposed that diurnal changes in diving depth of a southern elephant seal are related to the abundance of squid. Croxall et al. (1985), as well as Fraser et al. (1989), found the diving behaviour of fur seals closely related to diel changes in vertical distribution of krill, and Bengtson and Stewart (1992) suggested that the distinct diel pattern of dive timing and depth of creabeater seals may be related to possible predator avoidance behaviour by the seals' principal prey, Antarctic krill. Synchronisation of the seals' diving activity with

oscillations in the abundance of their prey would greatly increase the efficiency of the seals' foraging effort. Kaufmann et al. (1995) found a diel pattern in abundance of macrozooplankton and mikronekton in open water and ice-covered areas of the northwestern Weddell Sea suggesting a diel vertical migration that is particularly well developed beneath pack ice.

Furthermore, juvenile and adult *Pleuragramma antarcticum* are important pelagic prey fishes for Weddell seals (Plötz 1986; Plötz et al. 1991) in our study area. This fish species, as well as krill, has been identified from trawl samples beneath pack ice (Kaufmann et al. 1995). Trawl data from open-water areas, however, were unavailable for comparison in that study. The Weddell seal at our study area benefits from the trophic communities both under the fast ice and in the open-water areas of the Drescher Inlet. Assuming that activity patterns of the Weddell seal's prey beneath the ice might be different from those in the polynya areas, this would explain the existence of both the tidal activity pattern and the persisting very low amplitude circadian pattern in the seal's diurnal cycle of behaviour. Since we know from earlier investigations that Weddell seals usually remain inside the ice-covered inlet for their foraging activities (Plötz et al. 1995), we hypothesise that a tidal activity pattern for the seal's prey is more likely than a circadian pattern. If the Weddell seal had indeed the ability to coordinate feeding efforts with prey abundance, then this would provide further evidence for its high degree of adaptation to the coastal fast-ice environment. We conclude that the zeitgeber strength of tidal movements obviously overrides the cues provided by the light-dark cycle during polar summer. To decide whether the seals' behavioural pattern is learned as a result of experiencing greater foraging success, or innate, we propose to analyse the ontogeny of the diving behaviour and thermal rhythmicity of young Weddell seals with the help of time series analysis tools, together with a study on variations in abundance of prey species taken by Weddell seals in the same habitat.

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