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Haulout patterns of grey seals *Halichoerus grypus* in the Baltic Sea

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The haulout pattern of seals, i.e. the distribution of the time they spend on shore or on ice, may be influenced by a large number of extrinsic factors such as season, time of day and weather, as well as factors related to the animal's internal state. In this study we used a time-lapse video system at a haulout site, and satellite relay data loggers attached to 11 individual seals to monitor haulout pattern of grey seals *Halichoerus grypus* in the Baltic Sea during summer and early winter from 1989 through 1996. Time of day had the greatest influence on haulout patterns with the maximum numbers of seals ashore at night. Season and habitat specific characteristics also had important effects on haulout pattern. We suggest that diel changes in prey behaviour and distribution account for the nocturnal haulout pattern observed. The size of the population of grey seals in the Baltic Sea has been estimated by the number of seals ashore. Our results demonstrate the possibility of improving future estimates using a correction based on time of day.

Key words: Baltic Sea, diel pattern, grey seal, Halichoerus grypus, haulout pattern, satellite telemetry

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Phocid seals spend much of their time at sea. However, some of their time is spent ashore or on ice, a behaviour known as 'hauling out'. The frequency, duration, and time of day of hauling out are likely to be determined by a large number of interacting intrinsic and extrinsic factors. Intrinsic factors are those which depend on the physiological state of the seal (e.g. body condition, hunger, pregnancy) while extrinsic factors include time of day, date, weather, geographical position, availability of food. The interaction of these factors can result in complicated patterns of haulout behaviour.

Studies on species of phocid seals have suggested that the haulout pattern may be affected by factors such as time of day (Finley 1979, Allen, Ainley, Page & Ribic 1984, Stewart 1984, Yochem, Stewart, DeLong & DeMaster 1987, Lydersen 1991, Stewart & Yochem 1994), seasonality (Grellier, Thompson & Corpe 1996), tide (Cameron 1970), temperature (Watts 1992) and rain (Krieber & Barette 1984). Knowledge of haulout patterns in grey seals *Halichoerus grypus* in the Baltic Sea is limited, based primarily on reports from commercial fisheries (Zheglov 1973), or on studies of a single animal (Sjöberg, Fedak & McConnell 1995) or a single haulout site (Helle & Stenman 1990).

Counts of seals hauled out on land can be used to estimate population size (Eberhardt, Chapman & Gilbert 1979, Thompson, Tollit, Wood, Corpe, Hammond & MacKay 1996). In the Baltic Sea, grey seals are counted on haulouts regularly during the ice-free season (May - December) by various institutions in Sweden, Finland and Estonia. Counts are coordinated to be carried out during certain weeks, to provide an estimate of minimum population size (Helander 1995). The grey seal population declined in the Baltic from about 100,000 in the early 1900s to around 2,000 individuals by the late 1970s (Almkvist 1982). Recent surveys indicate that the population has since increased to at least 5,000. These estimates of abundance are, however, affected by variability in haulout pattern.

In this study we focus on the influence of extrinsic factors on haulout pattern of grey seals in the Baltic Sea. The study period ranged from June through January, between the moult (May - early June) and the breeding season (late February - March). Thus, we have avoided periods when intrinsic factors such as breeding or moulting condition are likely to have the greatest effects on the haulout pattern. The Baltic Sea has no measurable tide. However, water level may fluctuate due to weather conditions, but only slowly and irregularly and normally with an amplitude of less than one metre. We analysed haulout pattern in relation to the factors of *date*, *surf*, *temperature*, *time of day*, *water level*, *wind direction* and *wind speed*. We also analysed the haulout duration and calculated the proportion of study seals hauled out at different times of day. These calculations may be used to derive a correction factor (Thompson et al. 1996) to improve future population estimates.

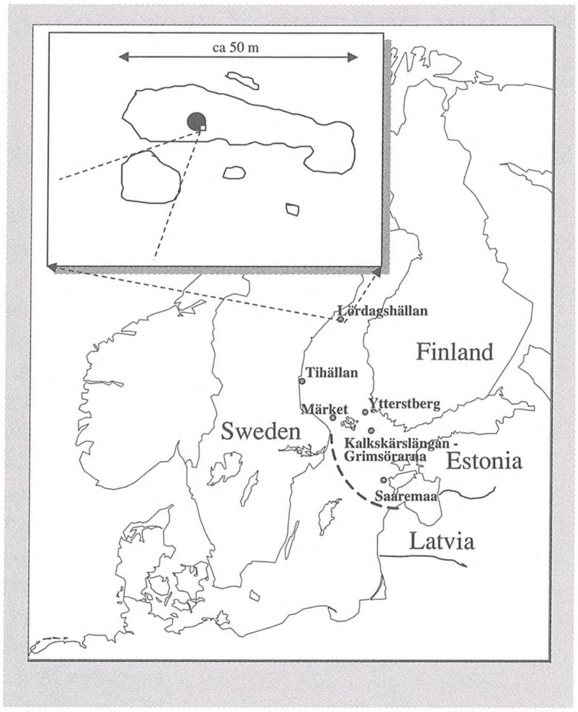

Figure 1. Major haulout sites visited by tagged seals in the Baltic. The dotted line in the middle of the Baltic Sea indicates the approximate southern limit of tagged seal movements during the study period. The inserted map shows the video study site and the view field of the camera.

Material and methods

We collected data on haulout patterns using two techniques: time-lapse video sequences at a single haulout site, and haulout data and locations of individual seals collected using Satellite Relay Data Loggers (SRDL) which used the Argos satellite telemetry system.

Video study

The video study was carried out during two periods, June - August 1989 and June - October 1992, on Lördagshällan (63°25'50" N, 19°54'00" E), a group of two small islands with several smaller rocks nearby (Fig. 1). The islands are located in open sea and comprise one of three major haulout sites in the area, with the next nearest being about 5 km away. A video camera (Panasonic M1) equipped with a time-lapse mechanism was housed in a waterproof box and powered by a 12V 60Ah battery. To avoid exposure to breaking waves during extreme weather conditions the video camera was fixed on a cairn 4.5 m above sea level. The area covered by the video camera was the entire area of the smaller of the islands, approximately 15 m from the cairn (see Fig. 1). The surveyed island is known to be a preferred haulout site for grey seals and has an area of approximately 100 m².

The time lapse mechanism recorded a video sequence between 10 to 30 seconds every 60 minutes, allowing records to be taken of up to 10 days in a row without supervision. The videotapes recorded the number of seals at the haulout site during daylight hours. Any vocalisations made by the seals (Barnes 1984) during all hours were also recorded on the videotape. Area covered by *surf* (estimated percentage of wave break covering haulout site) was also assessed from the videotapes. Data on *temperature*, *wind direction* and *wind speed* were obtained from Sydostbrottens lighthouse 16 km southeast of the haulout site. *Water level* data were collected from either Ratan or Spikarna water level measuring centre (Swedish Meteorological and Hydrographic Institute), 80 km north and 150 km southwest of the haulout site, respectively. A binary presence/absence variable was calculated which included as 'present' those sequences where only vocalisations provided an indication that there were seals hauled out. We also transposed *wind direction* to two new variables representing an *east-west* wind component and a *north-south* component.

Diel rhythm

The diel pattern was analysed by testing for significant deviation from a uniform diel distribution for each year, and for June and September separately, with Rayleigh's test of uniformity (Zar 1984, Fisher 1993, Kovach 1994).

Other extrinsic factors

The influence of the factors *date*, *surf*, *temperature*, *water level*, *wind direction* and *wind speed* on the haulout pattern was analysed with a generalised linear model. To minimise the dependency between observations one video sequence was sampled from the main video data set one hour (±30 minutes) before each sunrise.

We used two different regressions to analyse the influence of the factors on haulout pattern. Firstly, a logistic regression was used to analyse the influence of factors on whether seals hauled out or not, i.e. presence or absence of seals. Then, a Poisson regression was used to analyse the influences on the number of seals hauled out.

The maximal model for both regressions was assumed to be $\eta = \alpha + \beta_1 Date + \beta_2 Surf + \beta_3 Temperature + \beta_4 Water\ level + \beta_5 Wind\ direction_{\ East\text{-}west} + \beta_6 Wind\ direction_{\ North\text{-}south} + \beta_7 Wind\ speed.$

In the generalised linear model η (the linear predictor) is related to μ (the response mean) by a link function $\log\left(\frac{\mu}{\eta - \mu}\right) = \eta$ for the logistic regression and $\log \mu = \eta$ for the Poisson regression. Because of overdispersion in the Poisson regression, the data were weighted with Pearson χ^2/df (Crawly 1993). Collinearity within the model was analysed using the condition index (Belsley, Kuh & Welsch 1980). Parameters were tested for significance with a t-test, and improvement of deviance analysed using the log-likelihood ratio test (LLR-test)(Crawly 1993). To calculate an approximation of the correlation coefficient (r^2) for the maximal model, we used the formula

$$\left(1 - \frac{\text{Deviance}_{\text{maximal}}}{\text{Deviance}_{\text{null}}}\right).$$

Satellite monitored seals

In the satellite telemetry study, seals were caught during late summer 1992, 1993, 1995 and 1996 using tangle nets at the Tihällan seal sanctuary (61°28'00"N, 17°25'40"E) in the archipelago of Hudiksvall or near Lördagshällan (63°25'50"N, 19°54'00"E) outside Norrbyskär archipelago, Sweden (see Fig. 1). After capture, the animals were anaesthetised with Zoletil 100 (Baker, Fedak, Anderson, Arnbom & Baker 1990) and a satellite relay data logger (SRDL) (McConnell, Chambers & Fedak 1992, Fedak, Lovell & McConnell 1996) was glued to the fur on the seal's neck with a two-component epoxy glue (Fedak, Anderson & Curry 1983). A haulout was defined to have started when a submergence sensor on the SRDL had been continuously out of the water for more than 240 seconds and the end of a haulout was defined when the sensor had been continuously underwater for more than 40 seconds.

Diel rhythm

To produce a data set comparable with the video study for the diel pattern analysis, one observation each hour on the hour was extracted from the SRDL data. The diel pattern was tested for significant deviation from a uniform diel distribution, for each seal, from the entire period, and for September and December separately, using Rayleigh's test of uniformity. Differences in diel distribution between September and December were investigated with a χ^2-test for circular data (Kovach 1994). Difference between sunset/sunrise and start/end of haulouts were calculated and plotted to explore the influence of dawn and dusk on haulout patterns.

Haulout duration

A frequency distribution graph was made to visually assess the distribution of haulout durations. We also assessed the influence of season on haulout duration between September and December using a Wilcoxon paired sample test (Zar 1984).

Proportion of study seals hauled out

The proportion of seals fitted with SRDLs hauled out at any given time was calculated from haulout records. For each seal, 'hauled out' or 'not hauled out' was determined on the hour, throughout the day. The data were then grouped by period (each month or the entire period) and three-hour interval (e.g. 00:00, 01:00 and 02:00; 03:00, 04:00 and 05:00; ...). The number of hourly records when a seal was hauled out was expressed as a percentage of the total number of hourly records within a grouping. The means and standard deviations of the three-hourly percentages for seals that contributed at least 10 days for each analysed period were calculated for the different months and the entire period. To detect any difference in proportion of haulouts between months we used a Kruskal-Wallis test (Zar 1984).

'False haulouts'

Some haulouts apparently occurred at times when seals were located at sea (subsequently termed 'false haulouts'), either as a result of Argos location error (Type 1) or because the animals were keeping the sensor clear of the water for extended periods at times while at sea (Type 2). Type 2 'false haulouts' should be excluded, but Type 1 'false haulouts' may genuinely represent time spent ashore and excluding them would tend to bias estimates of haulout occurrence downward. We assume (an assumption corroborated by personal observations of seals at sea) that the probability of 'false haulouts' of Type 2 occurring would diminish with their duration because shifts of position by the animal in the water and splashes from waves would frequently end such periods. We examined the occurrence and extent of these 'false haulouts' in two seals that used one localised haulout area for the whole tracking period. We determined the proportion of haulouts at sea, for different minimum haulout durations by plotting the geographical position for each haulout and determining which appeared to occur at sea. The criterion for 'appearing to be at sea' was a location more than 10 km from land. A graph of the calculated proportion of 'false haulouts' was plotted against haulout duration to look for an inflexion point, below which haulouts could be rejected. A new data set was created using only haulouts longer than this minimum. We compared the new data set with the original data set to estimate how the occurrence of 'false haulouts' influenced our results.

Results

Video study

Time-lapse video sequences were recorded for 82 days in 1989 (6 June - 15 July and 17 July - 27 August) and for 112 days in 1992 (11 June - 7 July and 20 July - 12 October). We examined 4,572 video sequences (1,913 and 2,659 in 1989 and 1992, respectively). The number of seals hauled out on a single video sequence varied from zero to 157 ($\bar{x}$ = 26.8 in 1989 and $\bar{x}$ = 32.5 in 1992).

Table 1. Rayleigh's test for uniform distribution of hourly observations of haulouts over a 24-hour period (GMT). $\bar{x} \pm$ SD is given for each SRDL, for all SRDLs combined, for the most southeastern haulout site (outside Saaremaa), and for both video sets. Data are grouped by month (June, only video; September, except video 1989 which represents August; December, only for SRDL data) as well as for the entire study period.

	Total		June		September		December	
SRDL	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
1	*τ 22.45	04.24			*τ 22.20	04.10	*τ 00.29	05.43
2	*τ 01.16	04.40			*τ 00.33	03.14	*τ 02.24	06.04
3	*τ 00.27	05.01			*τ 00.25	04.04	*τ 23.56	05.05
4	*τ 01.38	06.22			*τ 02.17	05.38		
5	*τ 23.55	04.40			*τ 23.30	02.52	* 01.56	04.06
6	*τ 21.44	06.02			*τ 21.40	05.45	00.06	06.49
7	*τ 23.32	02.10						
8	*τ 22.26	05.02			*τ 22.20	03.33	*τ 22.03	06.04
9	*τ 23.05	05.35			* 23.27	05.28		
10	*τ 23.40	05.51			*τ 21.37	03.33	00.11	08.30
11	22.24	07.12			20.39	06.22		
All SRDLs	τ* 23.23	05.50			*τ 23.29	04.45	*τ 00.17	06.25
Saaremaa	τ* 23.59	03.58						
Video 1989	* 00.39	05.56	* 01.37	07.06	* 23.42	04.45		
Video 1992	* 00.06	06.56	* 01.26	08.01	* 23.10	06.43		

* Significantly different from uniform distribution P < 0.01.
τ Significantly different from uniform distribution P < 0.01 for haulouts with a minimum duration of three hours.

Diel rhythm

There was a demonstrable diel pattern to haulout behaviour. Rayleigh's test of uniformity showed a significant deviation from circular uniformity for both years with more haulouts during the night (Table 1). However, in June, the haulout pattern from the video study had a later mean hourly vector with a less distinct pattern than in September.

Other extrinsic factors

The video data set used in the generalised linear model consisted of 80 video sequences in 1989 and 110 video sequences in 1992. There were unusually high counts in late June and early July 1992 (Fig. 2), but in spite of these high counts there was no significant difference in numbers of seals hauling out between the two years (P = 0.85, Wilcoxon). Thus, we pooled the data. After removal of observations with missing data (e.g. no estimate of the number of seals present during darkness, no wind data), 167 observations remained. We found a low to moderate collinearity between the variables in the model and the condition index was 31.09 (Belsley et al. 1980). The condition index also indicated that *date*, *temperature*, and *water level* contributed to the variance of two or more other variables. This makes the evaluation of variables in the model less reliable.

Both in the logistic and the Poisson regressions, the maximal model differed significantly from the null model using the LLR test ($P < 0.001$) and the value for an approximated r^2 for the logistic regression was 0.28 and for the Poisson regression 0.38 (Tables 2 and 3).

In the logistic regression *surf* and *date* had significant negative effects on haulout behaviour (LLR test; $P < 0.0001$, $P < 0.0293$ and t-test; $P < 0.0001$, $P < 0.0333$). *Surf* alone had most influence. No other variables contributed significantly to the model (see Table 2).

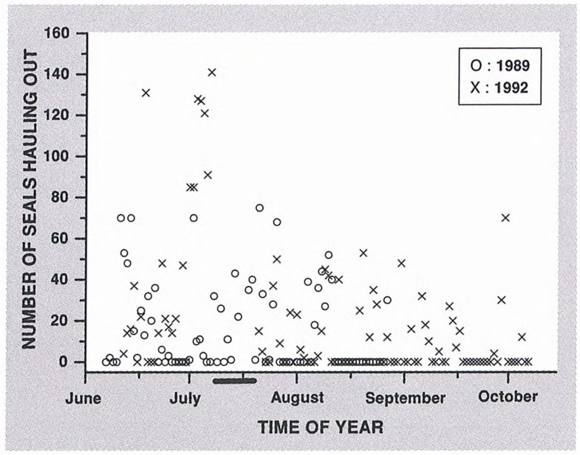

Figure 2. Number of seals hauled out one hour (±30 minutes) before sunrise as determined from time-lapse video records. The bold line under the X-axis indicates dates when data were not collected in 1992.

The Poisson regression showed that the number of seals hauled out was influenced by *surf*, *date*, and both *wind direction* variables. As in the logistic regression, *surf* made the largest contribution of all variables and date the second largest (see Table 3). The signs of the significant parameters were consistent between the Poisson and the logistic regression.

In summary, the video study showed that peak numbers of seals were ashore at night. *Surf* and *date* affected the decision of the seal to haul out. *Wind direction* also had a significant effect on the number of seals hauled out.

Table 2. Results from the logistic regression of the influence of explanatory variables on the presence/absence of seals at the haulout monitored by video. The maximal model includes all variables and the null model contains no explanatory data. The scaled deviance of an explanatory variable is the scaled deviance for the maximal model without that variable. The significance of the scaled deviance is calculated with log-likelihood ratio test. The regression coefficient's (β) significance is calculated using t-test. There are 160 degrees of freedom.

Model	Explanatory variables	Scaled deviance	Scaled deviance with variable removed	P	β	SE	P
				Explanatory variables			
Maximal model		167.09		0.0001			
Null model		232.30					
	Intercept				6.0884	2.3485	0.0104
	Surf (%)		200.64	0.0001	-0.0353	0.0070	0.0001
	Date		171.85	0.0293	-0.0174	0.0081	0.0333
	Wind (E-W)		169.55	0.1168	0.0059	0.0038	0.1226
	Wind (N-S)		167.87	0.3775	0.0029	0.0033	0.3809
	Wind speed		167.43	0.2915	-0.0447	0.3309	0.5660
	Temperature		167.33	0.6297	-0.0388	0.0805	0.6305
	Water level		167.33	0.6438	0.0080	0.2138	0.6463

Table 3. Results from the Poisson regression of the influence of explanatory variables on number of seals at the haulout monitored by video. The maximal model includes all variables and the null model contains no explanatory data. The scaled deviance of an explanatory variable is the scaled deviance for the maximal model without that variable. The significance of the scaled deviance is calculated with log-likelihood ratio test. The regression coefficient's (β) significance is calculated using t-test. There are 160 degrees of freedom.

Model	Explanatory variables	Scaled deviance	Scaled deviance with variable removed	Explanatory variables			
				P	β	SE	P
Maximal model		145.49		0.0001			
Null model		238.46					
	Intercept				6.1197	0.9389	0.0001
	Surf (%)		170.46	0.0001	-0.0211	0.0046	0.0001
	Date		152.46	0.0083	-0.0091	0.0035	0.094
	Wind (E-W)		151.94	0.0111	0.0050	0.0019	0.0102
	Wind (N-S)		151.87	0.0115	0.0040	0.0016	0.0135
	Temperature		148.35	0.0907	-0.0608	0.0036	0.0933
	Water level		147.63	0.1432	-0.0115	0.0077	0.1374
	Wind speed		145.49	1.0000	0.0001	0.0368	0.9991

Satellite monitored seals

We monitored the behaviour of the 11 seals equipped with SRDLs for 14-185 days ($\bar{x}$ = 112.8) and recorded 11-111 haulout events per seal ($\bar{x}$ = 72.1) (Table 4). These seals covered an area approximately from 58°N to 66°N and 17°E to 24°E (i.e. most of the northern part of the Baltic). They used six major haulout areas (Lördagshällan, Tihällan, Märket, Ytterstberg, Kalkskärslängan - Grimsörarna, and outside Saaremaa) (see Fig. 1). Three seals also visited smaller, less frequented haulout sites on occasion.

Diel rhythm

The SRDL studies showed a distinct diurnal haulout pattern with more haulouts recorded during the night. Rayleigh's test of uniformity showed a significant deviation ($P < 0.01$) from circular uniformity for all 32 tested distributions except in three cases (seal 6 and 10 in December, $P = 0.11$ and $P = 0.46$; seal 11 for the entire period, $P = 0.39$). The mean hourly vector for the different seals' haulout activity over the entire period as well as in September and December ranged from 21.37 ± 03.33 SD to 02.24 ± 06.04 SD (GMT)(see Table 1).

There was no significant difference in mean hourly vector between September and December for the different seals except seal 2 ($P = 0.03$). However, in December, the individual mean hourly vector was at a later hour and with a less distinct pattern (higher SD) than in September. The exception was individuals 3 and 8, which tended to haul out earlier in December. No difference in diel rhythm was apparent between the seals at different haulout sites. A plot of the diel haulout pattern in relation to time of sunrise and sunset indicates a clear relationship (Fig. 3). Haulouts tended to start close to sunset and end close to sunrise.

Haulout durations

Short haulouts (<1 hour) were most numerous, although most time ashore was spent during long haulouts. The frequency of longer haulouts decreased rapidly. Haulouts lasting more than 20 hours were rare (Fig. 4). Haulout duration increased significant-

Table 4. Sex, weight, dates, and number of haulouts of grey seals fitted with satellite relay data loggers (SRDLs). Start date is the date of the first recorded haulout and end date is the last date of a transmission from a SRDL. The numbers of haulouts for each seal is the number recorded by the SRDL during the entire tracking period.

SRDL	Sex	Weight (kg)	Start date	End date	Tracking duration (days)	Numbers of haulouts
1	♂	87	26-08-1992	15-12-1992	112	79
2	♀	85	06-08-1993	25-01-1994	173	104
3	♂	140	07-08-1993	17-01-1994	164	89
4	♂	135	06-08-1993	07-11-1993	94	94
5	♀	140	07-08-1993	04-02-1994	182	111
6	♀	68	16-08-1995	13-12-1995	120	79
7	♂	52	21-08-1996	03-09-1996	14	11
8	♀	42	14-09-1996	23-12-1996	101	61
9	♂	48	20-08-1996	02-11-1996	75	53
10	♀	64	25-07-1996	25-01-1997	185	97
11	♀	55	30-08-1996	19-09-1996	21	15

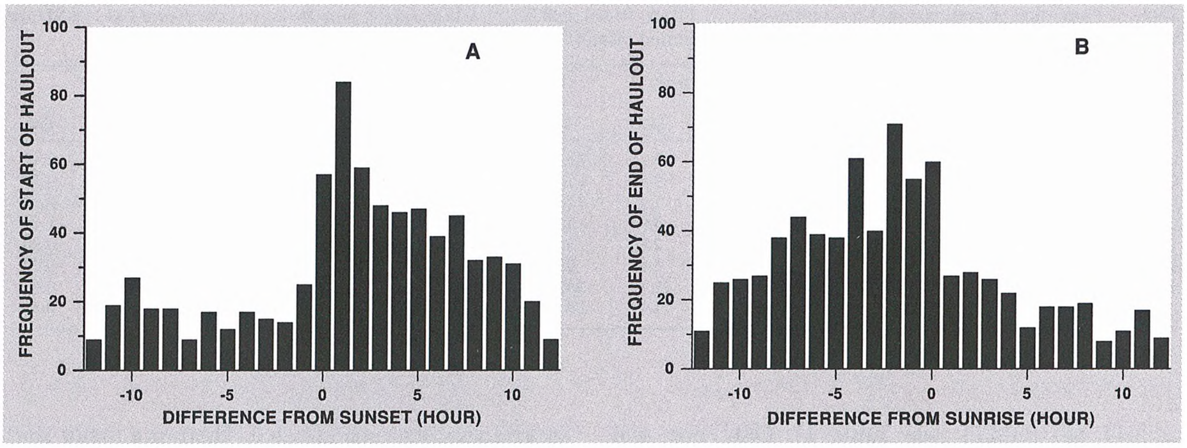

Figure 3. Start of haulouts in relation to sunset (A) and end of haulouts in relation to sunrise (B) for 11 SRDL-tagged seals.

ly from September to December ($P < 0.05$). The increase was more pronounced in smaller seals. Haulout events occurred at least twice as often per day in September than in December for all seals except seal 2 (seal 1 = 4.7, seal 2 = 1.3, seal 3 = 2.0 and seal 5 = 2.0, seal 6 = 2.8, seal 8 = 4.2, and seal 10 = 2.8).

Proportion of seals hauled out

The proportion of SRDL seals hauled out followed a similar diurnal rhythm. It was greatest during the two darkest periods of night 21:00 - 23:00 GMT and 00:00 - 02:00 GMT (+ 1 hour for local time) in all months (Table 5). There was one significant difference between months for comparable times of day (03:00 - 05:00, $P = 0.009$).

'False haulouts'

The proportion of 'false haulouts' decreased with increasing haulout duration, reaching a value of 0.07 at a duration of three hours (Fig. 5). We therefore used three hours as a minimum haulout duration to estimate the effect of 'false haulouts' on our data by examining the change in haulout parameters which resulted from omitting haulouts shorter than three hours.

In the reduced data set, all 32 tested diel distributions were significantly different ($P < 0.01$) from circular uniformity except in five cases: seal 6 and 10 in December ($P = 0.11$ and $P = 0.46$), seal 11 for total time tracked ($P = 0.39$), seal 5 in December ($P = 0.04$), and seal 9 in September ($P = 0.03$). The mean hourly vector ranged from 21.41 ± 5.56 SD to 02.25

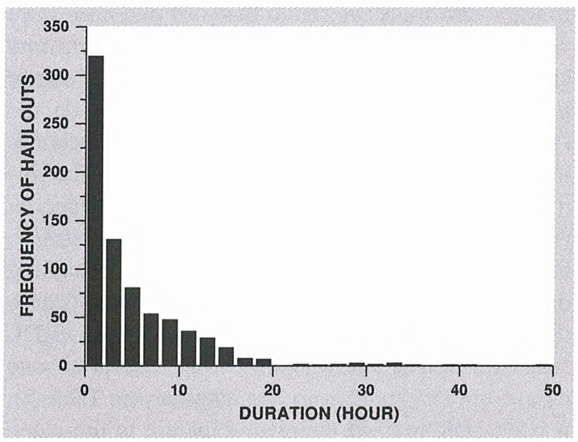

Figure 4. Frequency distribution of the durations of haulouts from 11 SRDL-tagged seals.

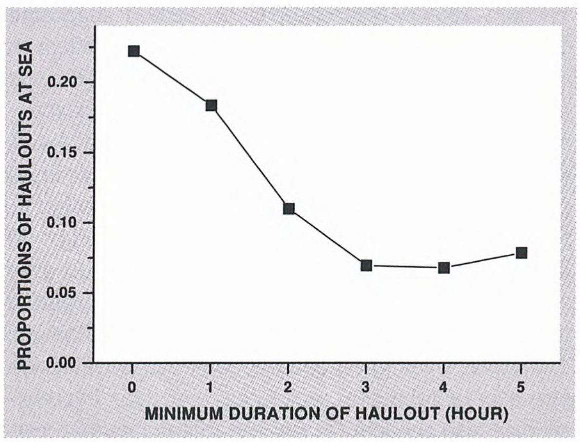

Figure 5. Proportion of haulouts recorded at sea ('false haulouts', see text) for different minimum haulout duration.

Table 5. Proportion of haulouts in 3-hour intervals (e.g. 00:00, 01:00, and 02:00; 03:00, 04:00, and 05:00; etc.) expressed as x̄ ± SD for all seals during August - November and the entire study period (Total). CV gives the coefficient of variance.

Hours used for assessing proportion of haulout (GMT)	Aug (N = 8)		Sep (N = 10)		Oct (N = 9)		Nov (N = 7)		Total (N = 11)		
	x̄	SD	x̄	SD	x̄	SD	x̄	SD	x̄	SD	CV
00:00, 01:00, 02:00	19.0	7.1	25.6	15.2	27.8	9.0	18.1	11.0	21.5	9.3	0.43
03:00, 04:00, 05:00 *	8.6	3.8	15.6	9.8	21.1	5.9	15.2	8.9	14.3	7.1	0.50
06:00, 07:00, 08:00	6.5	5.7	8.0	7.9	12.1	7.2	9.0	4.7	8.8	4.9	0.56
09:00, 10:00, 11:00	4.8	6.3	4.8	4.9	5.7	8.4	4.7	3.7	4.4	5.0	1.14
12:00, 13:00, 14:00	4.3	4.9	4.1	2.8	5.5	7.6	3.3	1.4	4.1	3.3	0.80
15:00, 16:00, 17:00	3.3	4.1	6.2	5.3	9.6	6.5	12.1	8.0	7.5	5.4	0.72
18:00, 19:00, 20:00	11.8	10.0	21.4	12.1	20.7	9.7	18.3	13.7	17.1	10.8	0.63
21:00, 22:00, 23:00	26.4	10.6	25.0	13.1	26.9	10.9	18.4	13.7	22.3	9.8	0.44

* Significantly different between month $P < 0.05$.

± 5.47 SD (GMT) (see Table 1). Only one seal changed significantly in its mean hourly vector between September and December (seal 2; $P = 0.03$).

The decrease in the proportion of study seals hauled out at any given time of day due to excluding haulouts of less than three hours was: August 9.3%, September 6.8%, October 1.8%, November 1.8% and for the entire period 3.6%.

Discussion

Diel rhythm

In contrast to most studies that describe peak numbers of seals hauled out during daytime (e.g. Finley 1979, Allen et al. 1984, Stewart 1984), we found that peak numbers of grey seals in the Baltic Sea hauled out at night. However, night-time haulout patterns have been recorded for Saimaa seals *Phoca hispida saimensis* (Hyvärinen, Hämäläinen & Kunnasranta 1995) and in some harbour seal populations (Thompson, Pierce, Hislop, Miller & Diack 1991, Stewart & Yochem 1994). Thompson et al. (1991) suggested that this nocturnal pattern is a result of a change in the behaviour of the harbour seal's prey (*Clupea* spp.). In the Baltic, herring *Clupea harengus* is abundant and, like the clupeoids in Scotland it forms schools near the bottom during the day but at night disperses in the water column in less dense schools. Söderberg (1974) found that the Baltic herring was the most commonly eaten prey in the Baltic grey seal's diet. Moreover, Sjöberg et al. (1995) reported that benthic feeding dives occurred during daytime. Therefore, we suggest that the nocturnal haulout pattern may be related to prey behaviour. This hypothesis may also account for the less distinct haulout pattern found in June. During summer when daylight is nearly continuous, the diel rhythm of several fish species appears to be affected. There is a major shift in the diel rhythm from either day or night activity, to a non-rhythmical or bimodal rhythm in June and July depending on fish species (e.g. Eriksson 1978, Müller 1978).

An alternative but less likely explanation for the diel haulout pattern might be avoidance of predators (e.g. Da Silva & Terhune 1988). Hunting of seals for profit (e.g. skin or bounty), or to reduce competition with fisheries has been a major factor in the decrease of the Baltic grey seal population during the 20th century. This may have affected haulout behaviour. Game animals have been reported to become more nocturnal as a result of human intrusion (e.g. Corbet 1960). However, general hunting has been banned for more than 20 years (since 1974) and hunting to protect fishing gear has been prohibited for over 10 years (since 1986). Consequently, we do not think the nocturnal haulout pattern of grey seals in the Baltic Sea has directly resulted from hunting by humans.

Other extrinsic factors

In the video study we found that *surf* and *date* were significant in the logistic regression, and *surf*, *date* and *wind direction* were significant in the Poisson regression. Also, there is consistency between the two regression models in that the same variables made the largest contributions to the model. The significant factors were primarily of a site-specific nature, such as *surf* and *wind direction*. Season (*date*) had significant negative influence on seals hauling out both in the Poisson and logistic model. Because the proportion of time spent hauled out by the SRDL seals did not decrease significantly, except in one case, from late summer to late autumn (see Table 5), it is possible that the decrease apparent in the video records reflects a change in haulout site rather than a change in haulout pattern. Also the time of each observation, which followed time of sunrise, may have contributed to the influence of season (date).

Although factors such as thermoregulation (Feltz & Fay 1966, Watts 1992) may influence haulout behaviour in some areas, we found that neither wind speed, nor ambient temperature influenced the haulout behaviour in this study.

Haulout duration

The duration of individual haulouts increased significantly between September and December. The increase was more pronounced in smaller seals. However, over this period, the daily haulout rate decreased in all but one small seal. If smaller seals are more susceptible to the severe weather that occurs in the latter part of the year they may delay the decision to haul out in severe conditions and compensate with longer haulouts when the weather improves (Brasseur, Creuwels, van der Werf & Reijnders 1996).

Proportion of seals hauled out - inferences for estimating population size

Estimates of the proportion of seals hauled out at a given time can be used, in combination with counts at haulout sites, to estimate the size of the population (Thompson et al. 1996). The optimum period to focus such efforts is when the proportion is the greatest and when the variability in both haulout proportions and counts is minimised. In their study of harbour seals, Thompson et al. (1996) used data collected during the pupping season. Our study in the Baltic Sea was carried out during a time of year where there were no such intrinsic factors affecting haulout behaviour. Within the daily cycle, our data showed that the proportion of seals hauling out was highest and the relative variability in proportion hauled out, as estimated by the coefficient of variation, was lowest at night (see Table 5). This implies that, during this time of year, counts at night may provide a better estimate of population size than counts during the day if variability in night-time counts is no greater than in daytime counts. Such night-time surveys would probably require image intensifiers or thermal imagers (Hiby, Duck, Thompson, Hall & Harwood 1996).

The effect of 'false haulouts'

'False haulouts' occurred regularly in our records, particularly among haulouts shorter than three hours in duration (see Fig. 5). We therefore omitted haulouts below this 3-hour minimum in order to decrease the effects of these 'false haulouts' on our estimates of true haulout behaviour and to produce a minimum estimate of the occurrence of haulout behaviour. However, this approach will ignore genuine short haulouts, which may be common in young seals, biasing our estimates downwards. In spite of this, we found that the effect of excluding haulouts of less than three hours did not affect our conclusions except for the proportion of seals hauling out in early autumn (August - September). The seemingly small influence of discarding haulouts with less than three hours is due to the fact that they contribute relatively little to total haulout duration. Also the technique of using only one data point each hour on the hour will discard many of the short haulouts (<1 hour).

We suggest that surveys of hauled out seals should be done in late autumn (October - November) due to the small influence of 'false haulouts' during that period. Nevertheless, the effect of 'false haulouts' on a survey is likely to be only a minor underestimation of the population if the surveys are conducted during the recommended period.

Conclusion

Grey seal haulout pattern is probably influenced by a complex interaction of intrinsic and extrinsic factors. It is therefore unlikely that any set of extrinsic factors alone can explain haulout pattern satisfactorily. Further, it is unlikely that any relationships found can be extended across species and environments, thus necessitating specific studies on different species and subpopulations.

The results from this study and consideration of the seal's life history suggest that future research should attempt to include the influence of intrinsic factors on haulout behaviour in conjunction with the study of extrinsic influences.

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