ACTIVITY AND HAUL OUT BEHAVIOUR OF CAPTIVE HARP SEALS (Pagophilus groenlandicus)

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Activity and Haul Out Behaviour of Captive Harp Seals (*Pagophilus groenlandicus*)

by

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Abstract

The annual cycle of all pinnipeds includes seasonal changes in behaviour linked to key events such as reproduction, moult, and in some species, migration. These changes in behaviour have generally been quantified in terms of haul out or diving, but rarely for more than one season. Weather conditions have been shown to influence the haul out pattern of some pinniped species but these studies have also had limited seasonal scope. This study measured activity levels (seal body movements per minute) and haul out behaviour of nine captive harp seals (*Pagophilus groenlandicus*) using modified time-depth recorders for a fourteen-month period. Solar radiation, temperature, wind velocity, and relative humidity were concurrently monitored throughout the study. The harp seal was selected for study because relatively little quantitative information exists for this species' behaviour and because circannual patterns in their food intake and energy demands have been detected.

Activity levels and amount of time spent hauled out varied seasonally for most harp seals, but individual variation often precluded generalization. However, certain trends occurred during key annual cycle events. Seals spent significantly more time hauled out, and time of day of haul out shifted closer to midday during moult. Increasing wind velocity had a negative influence on haul out during this time, whereas solar radiation had a positive effect. These behavioural responses to weather conditions are energetically beneficial to seals, because exposure to warm temperatures accelerates the growth of skin and hair. Activity significantly increased in only two seals during the breeding period. Seasonal patterns of daily activity and haul out were overlaid by circadian rhythms. Activity consistently peaked around midday and was lowest at night when seals were found to haul out. The midday feeding schedule probably acted as an "entraining" mechanism for these rhythms. This suggests that factors like habits of prey (i.e., availability or ease of access) may play a role in determining the daily activity patterns of harp seals in the wild. Although no conclusive evidence exists to support this idea, daily dive patterns of several other seal species and the behaviour of their prey suggest that it is true.

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List of Abbreviations and Symbols

Abbreviation/Symbol	Definition
pers. comm.	personal communication
unpubl. data	unpublished data
MJ	megajoule
cm	centimeter
m	meter
m^2	meter squared
km	kilometer
min	minute
h	hour
L	liter
°	degree
α	alpha

Chapter 1: Introduction

Seasonal variations in animal behaviour occur in response to pronounced seasonal fluctuations in the environment. Development of adaptive strategies to cope with changing environments is imperative for survival. Therefore, many biological activities are concentrated or restricted to times of the year when they are most likely to be successful. Since seasonal variation in environmental conditions normally increases with increasing latitude, annual rhythmicity is most clearly expressed in animals inhabiting temperate and Arctic zones (Gwinner 1981).

Pinnipeds (seals, sea lions, and walruses) which inhabit higher latitudinal regions have well-defined annual cycles, and the accurate timing of cycle events is vital for their survival. For example, northern fur seals (*Callorhinus ursinus*) of the Pribilof Islands, Alaska, give birth in early July; the only time of the year when weather conditions favor growth and survival of pups (Trites and Antonelis 1994). Other seasonal changes in behaviour occur around key events like breeding, moult, and in some species, migration. Changes in behaviour during these times have often been described in terms of activity level (activity, hereafter).

Initial investigations of pinniped activity focused on haul out at terrestrial sites or on ice during breeding and moult, when animals were readily observed (Smith and Hammill 1981; Kovacs 1987; Stewart 1987; Yochem et al. 1987; Thompson et al. 1989). More recently, the use of time-depth recorders (TDR) has provided continuous documentation of dive and haul out activity (Lydersen and Kovacs 1993; Sjöberg et al. 1995; Crocker et al. 1997). These observational and TDR studies have revealed that pinnipeds exhibit patterns of daily activity and haul out, but both approaches generally have had limited seasonal scope.

Variations in activity have been of interest to researchers in areas were pinnipeds are known to eat commercial species, because activity comprises an important component of pinniped energy budgets (Lavigne et al. 1982); prey consumption estimates based on bioenergetic models change in response to different activity estimates. The recent decline of cod (*Gadus morhua*) stocks in the northwest Atlantic (Hutchings and Myers 1994; Myers and Cadigan 1995; Myers et al. 1996) has led to questions about the impact of pinnipeds on these stocks. The harp seal (*Pagophilus groenlandicus*) has received the most attention because its population is greater than all other pinniped species in Newfoundland waters, with recent estimates of almost five million individuals (Shelton et al. 1995).

The annual cycle of harp seals has been well-documented (Sergeant 1965; Sergeant 1976; Ronald and Dougan 1982). Pregnant females haul out on pack ice off the coast of Newfoundland or in the Gulf of St. Lawrence from late February to mid March and give birth (Sergeant 1965). Pups are nursed for approximately twelve days and mating follows shortly thereafter (Kovacs 1987). During April and May, the seals haul out in aggregations and undergo their annual moult (Sergeant 1965). After this, a northward migration to western Greenland and the eastern Canadian Arctic occurs. The return southward migration commences in September, with individuals returning in January (Sergeant 1965). Quantitative information on haul out or aquatic activity has been limited (Stewart 1987; Lydersen and Kovacs 1993) to studies conducted during lactation. This paucity of information, coupled with concerns about the impact of harp seals on commercial fish stocks, makes this species an excellent subject for study of activity patterns. However, its marine lifestyle makes data collection in the wild difficult. The current study of captive harp seals provided an opportunity to acquire baseline activity and haul out data over a long period. Activity was defined as seal body movements (per unit time) both in and out of the water, and haul out as the amount of time spent out of the water. Data were collected as continuous 24-h records of activity and haul out over a fourteen-month period through the use of modified TDRs.

The main objectives of this study were to quantify seasonal and daily variation in activity levels and haul out behaviour, and to investigate the influence of weather on both harp seal activity and haul out.

Chapter 2: Method

Study Animals and Facility

This study was conducted at the Ocean Sciences Centre (OSC) of Memorial University of Newfoundland at Logy Bay, Newfoundland (47°38′ latitude, 52°40′ longitude). Seals in this study were classified into two groups. The resident group consisted of animals that had been born in captivity or had lived there before 1995. This included Babette, Jamie, Tyler, Victor, and Virgil. The new group consisted of animals captured as adults in 1995: Chelsea, Elmo, Mickey, and Rhonda (Table 1). The seals were usually fed thawed herring (*Clupea harengus*) *ad libitum* around midday. However, diet was varied occasionally as part of other studies (Appendix A). All animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care.

The study animals were housed in an outdoor compound with two 300 000 L holding tanks through which fresh sea water was pumped at ambient temperatures from Logy Bay. The tanks each measured 12.3 m in diameter and 2.5 m in depth, and were bordered by approximately 190 m^2 of wooden haul out decking.

Equipment

Behavioural activity was measured with Mk6 Time-Depth Recorders modified as activity recorders (ARs; Wildlife Computers, Redmond, Washington, 98052). The ARs recorded the number of times two mercury switches changed from the “off” to “on” state (“ticks”, hereafter). From a level position, the AR had to be rotated more than 45° about

Table 1. Summary of information on the study animals.

Group/name	Abbreviation	Sex	Age	Origin
Resident				
Babette	Ba	F	Adult	Captured as adult, 1989
Jamie	Ja	M	Juvenile	Son of Ba, born 16 March 1994
Tyler	Ty	M	Adult	Captured as whitecoat, 1990
Victor	Vc	M	Juvenile	Son of Ba, born 11 March 1993
Virgil	Vg	M	Adult	Captured as adult, 1991
New				
Chelsea	Ch	F	Adult	Captured as adult, 1995
Elmo	El	M	Adult	Captured as adult, 1995
Mickey	Mc	M	Adult	Captured as adult, 1995
Rhonda	Rh	F	Adult	Captured as adult, 1995

Note: F=female, M=male.

either the x- or y-axis for a tick to be recorded. The AR did not record ticks when rotated about the z-axis. Number of ticks per minute was used as the measure of activity in this study. Presence in or out of the water ("haul out", hereafter) was measured by the conductivity pins or salinity switch located on the top of the AR. When the conductivity pins were wet, a circuit was closed, and the ARs recorded ticks under the wet state (i.e., not hauled out). "Dry time" may have been underestimated because the salinity switch did not always distinguish wetness due to rain, fog, or salt water splash. However, ground-truthing of AR data with behavioural observations (see p. 20) revealed that the recording of haul out by ARs was never observed to be underestimated by more than 6 min in any environmental condition. Dry periods were only counted if they were 5 min or more in duration, to avoid counting long periods seals spent at the water surface as periods of haul out. Involuntary haul out due to tank cleaning and other human disturbances were excluded from analysis.

ARs were attached to the pelage along the upper dorsal midline, using 5-minute marine epoxy (Industrial Formulators of Canada Ltd., Burnaby, B.C., V5C 3H9) or Loctite Superbonder (Loctite Corp., Mississauga, Ont., L4Z 1S6). ARs measured 7 cm in length, 6 cm in width, and 1.5 cm in height. Comparisons of seal behaviour (see p. 20), with and without ARs, did not indicate any influence of the ARs on behaviour.

Collection of Data

Data were collected from 13 September 1995 to 21 October 1996. Animals had ARs on their backs for continuous periods ("deployment periods", hereafter) ranging from 3 to 69 days between removals for downloading data. Appendix B summarizes deployment dates for each seal. Data from ARs were transferred into an ASCII file on a personal computer via a RS232 connection after ARs were removed from the seals' back. In addition, I kept a log of human disturbances caused by maintenance activities (feeding, cleaning, etc.). Such disturbances usually occurred between 0900 h and 1600 h.

Structuring of Data

Raw data (ticks $\cdot$ min^{-1} and dry or wet status $\cdot$ min^{-1}) were converted into two other databases. These data were half-hourly means and daily means of ticks $\cdot$ min^{-1} and dry or wet status. This permitted data analysis of both daily and seasonal patterns of activity and haul out. These databases were further divided by season, moult state, breeding condition, deployment period, and diurnal-undisturbed data (Table 2, Fig.1). Throughout this study, activity is referred to as total activity (includes body movements when seals were both in and out of water; is often interchanged with "activity") or aquatic activity (body movements when seals were only in water). Activity variables include: TK-MIN, TK-HH, TK-H, TK-D, TKW-HH, and TKW-D. Haul out variables include: ONDECK-HH, ONDECK-H, ONDECK-D, MOVE, TODECK, TOWATER, HAULOUTS, TIMEMAX, and TIMEMIN. These variables are defined in Table 2.

Records were kept on moult. Dates of initial loss of hair and skin (start of moult) and full emergence of new coat (end of moult) were noted for each individual (Table 5). During peak loss of hair, ARs could not be kept on for extended periods of time, so data were limited to four animals. The same number of non-moult days as available moult days were selected approximately one week after the full emergence of a new coat was observed. This permitted statistical comparisons of activity and haul out between moult and non-moult periods. Table 3 summarizes available moult and corresponding non-moult data for the seals.

Data Analysis

Most statistical analyses were performed using SAS Version 6.12 (SAS Institute Inc. 1993). Circular statistics were performed using Oriana Version 1.0 (Kovach 1994). The probability level accepted for a significant difference was $\alpha = 0.05$. Standard deviations (±1) are given as the measure of variation about the mean. Additional details, specific to different analyses, are presented in the appropriate chapters.

Table 2. Activity and haul out variables and data sets used in the study.

Variable/Data set	Definition
TK-MIN	Ticks $\cdot$ min^{-1}
TK-HH	Mean half-hourly sum of ticks, expressed as ticks $\cdot$ min^{-1}
TK-H	Mean hourly sum of ticks, expressed as ticks $\cdot$ min^{-1}
TK-D	Mean daily sum of ticks, expressed as ticks $\cdot$ min^{-1}
TKW-HH	Mean half-hourly sum of ticks excluding haul out, expressed as ticks $\cdot$ min^{-1}
TKW-D	Mean daily sum of ticks excluding haul out, expressed as ticks $\cdot$ min^{-1}
ONDECK-HH	Per cent of half hour hauled out
ONDECK-H	Per cent of hour hauled out
ONDECK-D	Per cent of day hauled out
MOVE	Event of moving to or from water to deck, or vice versa, per half-hour. This variable includes both TODECK and TOWATER
TODECK	Event of moving from water to deck
TOWATER	Event of moving from deck to water
HAULOUTS	Number of periods > 5 min duration that seals were hauled out, expressed as number per day
TIMEMAX	Time of day when highest level of activity was recorded, expressed as a half-hour period
TIMEMIN	Time of day when lowest level of activity was recorded, expressed as a half-hour period
Season	Fall (21 September – 20 December) Winter (21 December – 20 March) Spring (21 March – 20 June) Summer (21 June – 20 September)

Table 2. (continued)

Breeding/Non-breeding	Breeding (15 February – 20 March) Non-breeding (21 December – 23 January)
Moult/Non-moult	[a]Moult – period of hair loss and growth [a]Non-moult – period outside of moult
Deployment period	[b]Period of AR deployment, expressed in days
Diurnal-undisturbed data	Data excluding night (solar radiation < 0.01 $MJ \cdot m^{-2}$) and times of known human disturbance

[a] unique to individual seal (see Table 3)

[b] unique to individual seal (see Appendix B).

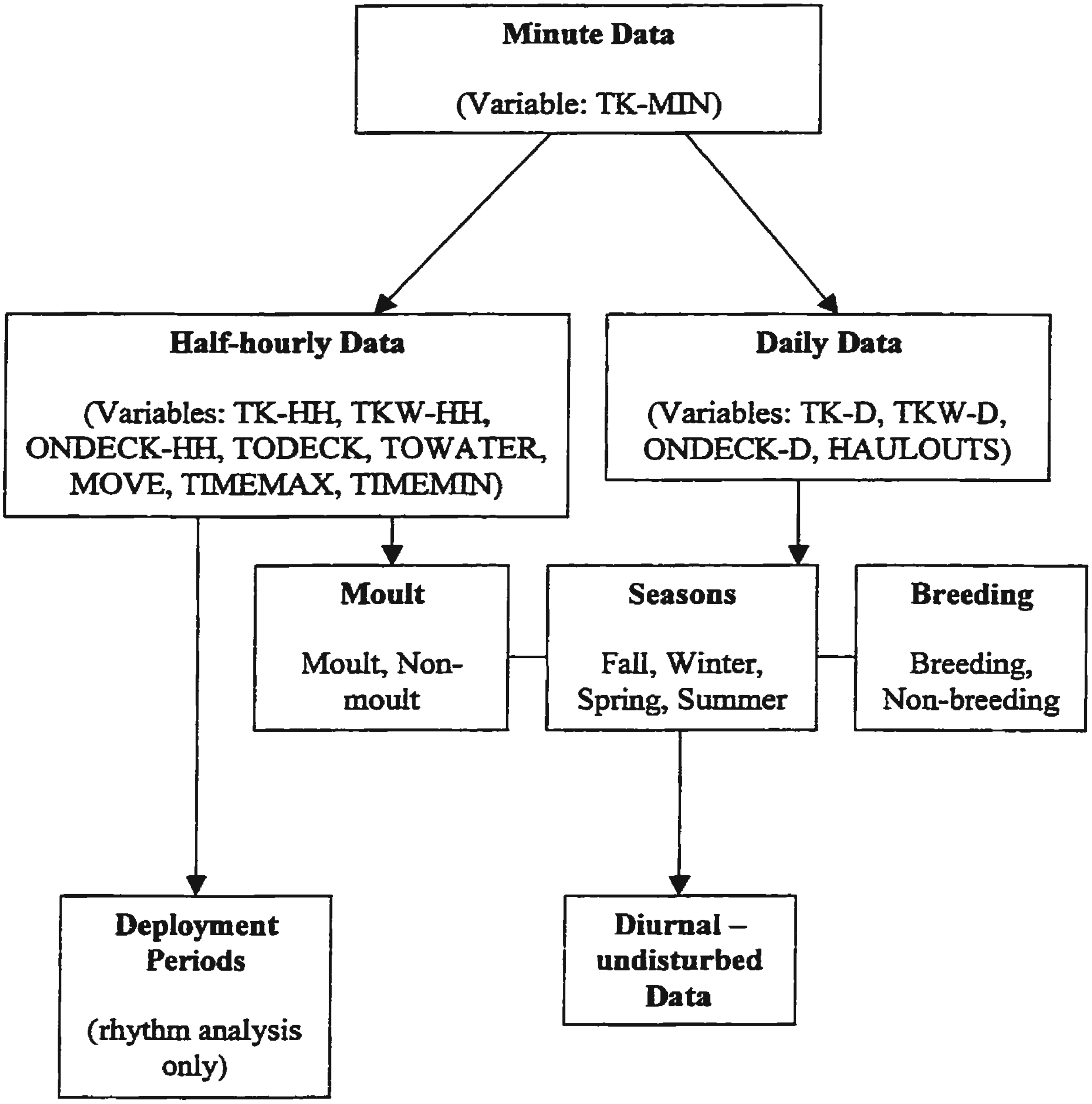


Figure 1. Data structure and variables used in this study.

Table 3. Summary of available data for moult and non-moult periods for four seals.

Seal	Moult	Non-moult
Ba	4 - 6 April; 30 April - 10 May	17 - 31 May
Mc	22 - 25 May	1 - 4 June
Rh	11 - 13 June	20 - 22 June
Vg	8 - 11 April; 15 - 16 May	20 - 25 May

Chapter 3: Seasonal and Daily Variation in Captive Harp Seal Activity and Haul Out

Introduction

Annual cycles in behaviour and physiological functions are common in animals exposed to seasonally variable environments (Gwinner 1981). Phocids exhibit pronounced behavioural and physiological changes during lactation, breeding, and moult. Females haul out to give birth and to undergo a lactation period that varies interspecifically in duration (4 to 50 days; Boness et al. 1994). During this time, pups rapidly gain mass and nutritional independence (Boness et al. 1994). Copulation occurs after lactation and most phocids copulate in the water (Stirling 1975; Merdsoy et al. 1978). In many species, adult males use aquatic displays and interactions to establish copulatory privileges (Ray 1967; Ray and DeCamp 1969; Stirling 1973; Kaufman et al. 1975; Sullivan 1981; 1982; Bartsh et al. 1992; Perry 1993). Females may choose to mate with a male based on his aquatic display, and males probably copulate with more than one female (Sullivan 1981; Bartsh et al. 1992). After the breeding period, phocids haul out to moult their skin and hair (Harrison and King 1965).

Harp seals exhibit similar behaviour patterns (Mohl et al. 1975; Merdsoy et al. 1978). Females give birth around late February to mid March (Sergeant 1965) and pups nurse for approximately twelve days (Kovacs 1987). While females suckle their pups, adult males display aquatically by making vigorous movements with their fore-flippers, vocalizing, and blowing streams of air bubbles from their nares (Mohl et al. 1975;

Merdsoy et al. 1978). Towards the end of lactation, females begin copulating (Sergeant 1976; Merdsoy et al. 1978). Courtship behaviour involves fore-flipper caressing, swimming ventrum to ventrum, and subsequent copulation (Merdsoy et al. 1978). It is believed that harp seals are polyandrous as many males have been observed to mate with one female (Merdsoy et al. 1978). Following the breeding period, harp seals haul out to moult their skin and hair (Harrison and King 1965; Sergeant 1976; 1991). This species exhibits age and sex differences in the timing of moult. Immature seals (age 0-5 years) and adult males generally moult first (late March to early April), followed by adult females (Sergeant 1965; 1991).

Changes in frequency or character of phocid behaviour often occur during lactation, mating, and moult. Generally, seals have been described as being active when in the water and inactive when hauled out (Fay and Ray 1968; Cameron 1970; Thompson et al. 1989). This approach to describing activity can be inaccurate because seals can be inactive (sleeping) in the water (Ridway et al. 1975), and active while hauled out (Anderson 1978: Merdsoy et al. 1978; Renouf and Lawson 1987). This study is unique in that activity was recorded continuously as seal body movements (per unit time) both in and out of the water, and haul out as the amount of time spent out of the water. The use of ARs permitted collection of unbiased data because an observer was not needed (i.e., inaccurate observations due to observer presence, fatigue, or bias were avoided).

In this study, annual cycle events of harp seals were limited to breeding and moult; captivity precluded migratory behaviour, and maternal behaviour did not occur as there were no live births during the study period. Breeding behaviour was restricted to the seven adult seals. Previous studies of captive harp seals recorded seasonal variations in physical composition, blubber, energy intake, and metabolism (Renouf et al. 1993; Renouf and Gales 1994). These variations have also been noted in captive harbour seals (*Phoca vitulina*; Renouf and Noseworthy 1990; Rosen and Renouf 1997), accompanied by seasonal changes in activity (Renouf and Noseworthy 1990; Rosen 1995). Captive harbour seals showed a significant increase in aquatic activity during breeding and a decrease during moult (Rosen 1995), similar to that reported for harbour seals in the wild (Sullivan 1980; 1981; 1982; Thompson 1988; Thompson et al. 1989; Perry 1993). The decrease in aquatic activity during moult occurred because animals increased their time spent hauled out. Pinnipeds spend more time hauled out during moult because radiation is used to synthesize vitamin D that is required for hair growth (McLaren 1958), and heating of the skin accelerates the moult process (Feltz and Fay 1966; Fay 1982). In light of these findings, I predicted that captive harp seals would decrease their activity levels during moult and increase the amount of time spent hauled out, and that sexually mature seals would exhibit the highest levels of activity during the breeding season when aquatic displays and interactions occurred.

Seasonal variations in activity and haul out behaviour occur because daily patterns change over time. Many studies of pinnipeds have focused on patterns of daily haul out (Smith and Hammill 1981; Kovacs 1987; Stewart 1987; Yochem et al. 1987; Thompson et al. 1989). The species studied most frequently is the harbour seal, which exhibits seasonal and geographical variation in such behaviour (Thompson et al. 1989; Boness et al. 1994; Grellier et al. 1996). In Orkney, Scotland, both males and females haul out in a marked diurnal pattern during the breeding and moult periods. Haul out mainly occurred from midday to late afternoon. During the winter, seals spent more time in offshore waters and they showed no marked diurnal haul out pattern (Thompson et al. 1989). In contrast, harbour seals at a more southerly location, San Miguel Island, California, exhibit diurnal patterns of haul out in both winter and summer. Stewart (1984) found that seals hauled out primarily between 1300 h and 1600 h, although a study at the same site during fall showed that nearly as many haul out bouts began at night as during the day (Yochem et al. 1987). Kelly and Quakenbush (1990) found distinct daily patterns of haul out behaviour that shifted seasonally in ringed seals (*Pusa hispida*); in March and April, seals hauled out in the evening and early morning, and in May and early June they hauled out mostly at midday. These seals also increased the amount of time spent hauled out as the spring progressed and moult occurred. There are indications that lactating female harp seals prefer to haul out in the daytime during periods of maximal solar radiation (Kovacs 1987; Stewart 1987). However, these studies included observations only during the daylight hours and would not have detected nocturnal haul out. Kovacs (1987) found that peak periods of haul out were during the first (0800-0900 h) and last (1600-1700 h) 1-h periods of her study. This suggests that nocturnal haul out occurs, at least in lactating females. Contrary to previous reports (Sergeant 1973; Ronald and Dougan 1982), harp seal haul out occurs outside the lactation and moulting periods in both the northwest Atlantic (G. Stenson, unpubl. data) and Barents Sea (T. Haug, pers. comm.) populations. Therefore, an objective of this study was to document time of day when animals haul out and return to the water, throughout the year. I predicted, that like ringed seals, harp seals would haul out around midday, during moult, when conditions are optimal for new skin and hair growth (Feltz and Fay 1966; Fay 1982; McLaren 1958).

Quantitative information about aquatic activity of harp seals has been limited to a single field study conducted on four lactating females (Lydersen and Kovacs 1993). Although this showed that mothers dove during lactation, it did not present evidence of daily dive patterns (and haul out) due to its limited sample size. Other studies have yielded more conclusive results and demonstrated interspecific variation in time of day when most diving occurs (Kooyman 1975; Thompson et al. 1991; Bengston and Stewart 1992; Crocker et al. 1997). Ringed seals and crabeater seals (*Lobodon carcinophagus*) tend to dive primarily at night while Weddell seals (*Leptonychotes weddellii*), northern elephant seals (*Mirounga angustirostris*), and grey seals (*Halichoerus grypus*) dive more during the day (Kooyman 1975; Lydersen 1991; Bengtson and Stewart 1992; Crocker et al. 1997). Daily patterns of pinniped diving behaviour may be a function of daily migration and distribution characteristics of their prey (Boulos and Terman 1980). For example, Baltic grey seals' principle prey, herring, form dense schools only during the day. Grey seals dive during the day and forage on these schools, probably to limit foraging costs (Sjöberg et al. 1995).

In this study, the seals did not actively forage but were subject to a feeding schedule. Daily feeding schedules can entrain circadian activity rhythms (Edmonds and Adler 1977), so I predicted that feeding time (near noon in this study) would act as an "entraining" influence for the circadian rhythms of these captive animals, and that peak activity levels would occur at this time as the seals began to anticipate food (Bolles and deLorge 1962). Another prediction was that these daily patterns in activity would not change during the study.

In the past, it was thought that both post-weaned phocid pups and lactating females (Boness et al. 1994) underwent periods of fasting. However, both Sergeant (1973) and Stewart and Murie (1986) found identifiable stomach contents in lactating harp seals, and Lydersen and Kovacs (1993) found that females dive during lactation. Other lactating phocids such as grey seals, hooded seals (*Cystophora cristata*), and northern elephant seals do fast (Fedak and Anderson 1982; Costa et al. 1986; Bowen et al. 1987). Moult was believed to be a time of fasting in harp seals (Ronald and Dougan 1982), but stomach contents of wild harp seals collected during moult often contain crustaceans (Wallace and Lawson 1997) and captive studies indicate that food intake merely decrease (Renouf et al. 1993). However, harp seals in this study were exposed to imposed periods of fasting as part of an assimilative and digestive efficiency study (Lawson et al. 1997, in press). Little attention has been given to activity during fasting periods as most studies have focused on mass loss and change in metabolic rate (Worthy and Lavigne 1987; Markussen et al. 1992; Rea and Costa 1992; Slip et al. 1992). It has been postulated that organisms whose life histories require fasting will lower a metabolic set point so as to prevent them from behaving like hungry animals (Mrosovsky and Sherry 1980), which typically become more active, thereby burning energy, when food-deprived (Milner 1970). Renouf and Noseworthy (1990) found that locomotor activity in captive harbour seals varied directly with food intake. In accordance with these findings, I hypothesized that harp seal activity would decrease during periods of forced fasting.

Both sexual and individual differences in activity and haul out have been noted in several species (Cameron 1970; Arnold and Trillmich 1985; Thompson and Rothery 1987; Thompson et al. 1989; Rosen 1995). Individual variation can be as distinct as some individual harbour seals preferring to haul out in the day and others at night (Yochem et al. 1987; Thompson et al. 1989). Therefore, I expected individual seals to differ in both activity and haul out measures.

Method

Ground-truthing Data from ARs

Direct observations were made throughout the study period on behaviour of individual seals to ground-truth AR data. An ethogram was constructed (Appendix C) based upon preliminary observations. These behavioural categories were later used in focal sampling (Altmann 1974). Observations were made from 0530-2100 h (when light levels were sufficient for accurate observations) to control for possible changes in behaviour due to time of day. The duration of observational periods varied throughout the study period, ranging from 10-30 minutes in length. The frequency and relative proportion of time spent performing each behaviour type was entered into a database that contained corresponding TK-MIN data. Pearson's correlation coefficients were calculated for all behavioural categories and TK-MIN (240 min of observations for each seal were used) to determine which behaviour types best predicted activity values.

Circadian Rhythms

Three approaches were used to detect possible rhythms in activity (TK-HH). Initially, a stepwise autoregression procedure (AUTOREG; SAS Institute Inc. 1993) was conducted on TK-HH for each deployment period for each seal. A lag of n=50 was used because I expected a 48 half-hour (24 h) rhythm. The test sequentially removed insignificant autoregressive lags until remaining lags had significant *t*-test results. Significant *t*-test results indicated correlation between the first TK-HH value and the TK-HH value corresponding to the significant lag. Lags (1-50) were grouped (4-11, 12-19, 20-27, 28-35, 36-43, 44-50) to produce a histogram of per cent significant lags ([no. significant lags/(no. lags in group) (no. deployment periods)](100)) versus lag groups. These plots provided a method of concisely presenting the rhythm results.

Secondly, spectral analysis (SPECTRA; SAS Institute Inc. 1993) of TK-HH was done for each deployment period (> 5 days) of each seal. Estimates of spectral density were used to create periodograms (spectral density versus period). These plots indicated how oscillations of different wavelengths contribute to the total variance of the time-series. To prove that these patterns (TK-HH) were not simply noise, a White Noise test was completed on data from each deployment period for each seal (SAS Institute Inc. 1993).

A third statistical approach was employed to test whether circadian activity (TK-HH) rhythms varied seasonally. A multiple regression fit program (Klemfuss and Clopton 1993; see Appendix D for details) was used to summarize circadian rhythms during winter and summer (n=1000 for each season) for five seals (Ch, Mc, Rh, Ty, Vg). Amplitude, mesor (rhythm average), computative acrophase (lag from midnight of day one to peak activity time), and its confidence interval (p=0.05) were calculated. F-ratios were also calculated to provide estimates of the significance of the fitted curve.

Seasonal Variation

Kendall's coefficient of concordance was used to test the null hypothesis that several related samples (in this case: TK-H and ONDECK-H) were from different populations (seasons, breeding, and moult periods). The coefficient (W) tested for agreement among rankings of hourly (24) activity and haul out values.

A Watson's F-test (Watson and Williams 1956) was used to test the null hypothesis that mean time of day for TIMEMIN, TIMEMAX, TODECK, and TOWATER were equal for each season, breeding, and moult period, for each seal and for pooled data. The F-statistic is the same as Fisher's variance ratio that is commonly used in linear statistics (including analysis of variance tests (ANOVAs)). Before each test, a third of the observations in the data set were selected randomly to eliminate the autocorrelation component introduced by sequential sampling. Mean time of day (rounded to the nearest hour) and circular standard deviations (Fisher 1993) were calculated and summarized according to season, breeding, and moult periods for all four response variables, for each seal, for all seals (pooled data across seasons), and for seasons and periods (pooled data across seals).

TK-D and ONDECK-D were averaged for each seal and for all seals (pooled data) across each season, breeding, and moult period. To compare TK-D and ONDECK-D a third of the observations in the data set were randomly selected to eliminate the autocorrelation component introduced by sequential sampling. A comparison of all the data and the third randomly selected, revealed that autocorrelation had been removed (PROC AUTOREG; lag n=1; SAS Institute Inc. 1993). A one-way ANOVA procedure was used to test for significant differences in TK-D and ONDECK-D (arcsine-transformed) for each seal and all seals across seasons, breeding, and moult periods. An additional analysis was used to test which paired seasons were significantly different from one another (GT2 method, GLM procedure; SAS Institute Inc. 1993).

Individuality, Sex, and Captivity Status Groups

The relative frequency of HAULOUTS (0 to 5+) was calculated as percentage of total study days, for individual seals, resident and new groups, and for all seals. The influence of sex and captivity status on TK-D (one-way ANOVA), TIMEMIN (Watson's F-test), TIMEMAX (Watson's F-test), ONDECK-D (one-way ANOVA), TODECK (Watson's F-test), TOWATER (Watson's F-test), and HAULOUTS (Kruskal-Wallis test) were investigated for the entire study period. The same tests were performed to test for variation among individuals, but analyses were also done exclusively on breeding/non-breeding and moult/non-moult data. A third of the observations in the data set were selected randomly to eliminate the autocorrelation component introduced by sequential sampling.

A binomial test was used to determine if all resident seals moulting before all new seals could occur by chance alone.

Prey Type and Food Intake

Animals were fed around midday every day. The standard diet was whole Atlantic herring supplemented with vitamins (Geraci 1975). Food for each seal was weighed to the nearest gram (g). The diet varied throughout the study period as part of a study on assimilative and digestive efficiency (Lawson et al. 1997, in press). Other prey types offered were: capelin (*Mallotus villosus*), Atlantic cod (*Gadus morhua*), Arctic cod (*Boreogadus saida*), redfish (*Sebastes marinus*), American plaice (*Hippoglossoides platessoides*), sand lance (*Ammodytes dubuis*), squid (*Illex illescebrosus*), and Greenland halibut (*Reinhardtius hippoglossoides*). The feeding trials were often preceded by a fast of 1-10 days. However, not all seals were involved in the feeding trials. Appendix A summarizes the feeding schedule for each seal.

To test for the effect of daily food intake (g) on activity (TK-D) I used PROC AUTOREG (lag n=1; SAS Institute Inc. 1993) to account for any first order autocorrelation in the data. These analyses were done for the entire duration of the study period, and for individual seals. The influence of prey type (excluding involuntary fasts) on activity was investigated by using a GLM of TK-D against food type and date.

Activity levels (TK-HH) during two periods of fast (13-21 September for Mc; 11-20 October for Mc and Ch) were compared with a regular feeding period on herring (11 November - 1 December for Mc; 11 November - 22 December for Ch). Data were subsampled to include activity from 0000 - 0600 h and 1000 - 1600 h. This allowed for comparison of results during no disturbance (0000 - 0600 h) and highly disturbed (1000 - 1600 h) periods. Kruskal-Wallis analyses were performed to compare TK-HH between fasting and feeding during these two 6-h periods.

Results

Ground-truthing Data from ARs

All seals spent much time below the water surface, making observations of their behaviour difficult. Activity (TK-MIN) was positively correlated with BE duration (Appendix C) for four of nine seals (Ch: r = 0.22; El: r = 0.60; Mc: r = 0.24; Vc: r = 0.23). For two seals, there were negative correlations between activity and BE frequency (Ch: r = -0.22; Mc: r = -0.37). Durations of three behavioural categories were negatively correlated with activity in a few cases: UP (Mc: r = -0.33; Ty: r = -0.76), DF (Ba: r = -0.31), and MV (Ch: r = -0.41).

Circadian Rhythms

All analytic approaches confirmed the presence of circadian rhythms. Stepwise autoregression revealed higher percentages of significant lags in the 4-11, 20-27, and 44-50 half-hourly lag groups for Vg (Fig. 2). Similar trends were found for the other seals. High autocorrelation in lags 4-11 is probably due to its proximity to lag 1. Lags 20-27 usually showed opposite *t*-value "directions" than lags 4-11 and lags 44-50 (Appendix E). Fig. 3 shows a typical periodogram (Appendix F). The sharp peak in spectral density at period 48 indicates a 48 half-hour (24 h) rhythm. White Noise tests indicated that no patterns could be attributed to noise.

Time of peak activity ranged from 10.6-13.6 h after midnight, and was later in the day during winter than the summer by approximately 1 h for all five seals (Table 4). However, winter acrophase values fell outside of the summer acrophase confidence

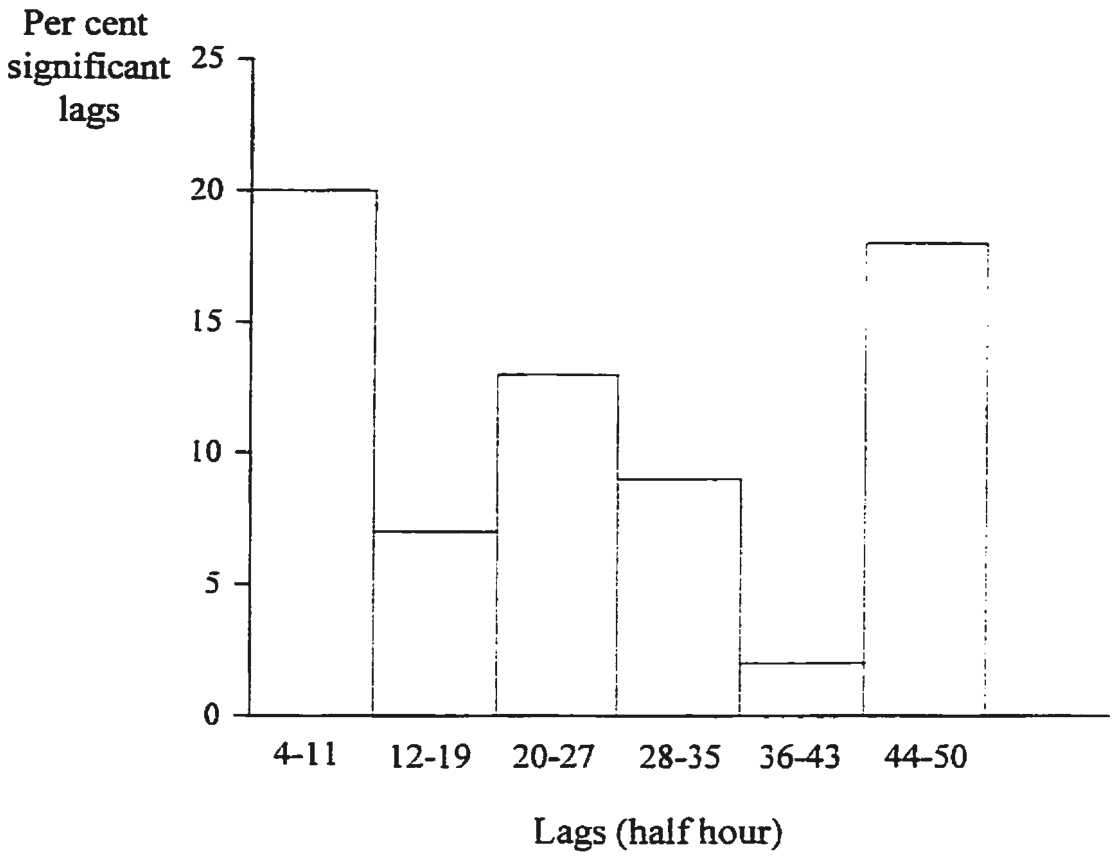


Figure 2. Percentage of significant lags in each lag group found in stepwise autoregression of Virgil's half-hourly activity data (TK-HH).

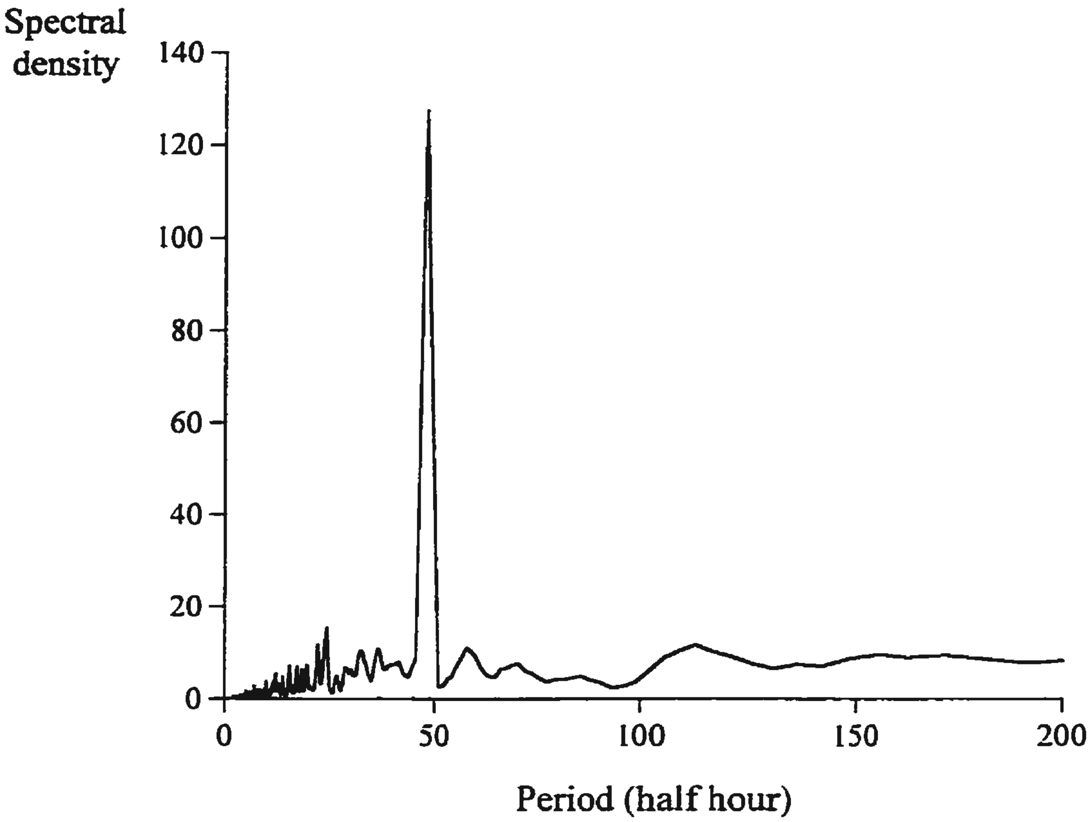


Figure 3. Activity (TK-HH) periodogram for Chelsea (13 August-19 October 1996) showing a peak in spectral density at period 48.

Table 4. Summary of circadian rhythms for five seals during summer and winter and results of fitted curve analysis.

Seal	Season	Mesor	Amplitude	Acrophase	(95 % C.I.)	F-ratio
Ch	Summer	8.64	1.29	11.7	(10.4 - 13.0)	2.75*
Ch	Winter	10.54	2.89	12.3	(11.5- 13.0)	8.15*
Mc	Summer	5.41	1.21	10.6	(9.8 - 11.4)	6.50*
Mc	Winter	2.77	1.63	11.6	(11.0 - 12.2)	12.5*
Rh	Summer	6.27	2.25	10.9	(10.0 - 11.9)	4.83*
Rh	Winter	3.63	1.00	11.6	(10.8 - 12.4)	6.98*
Ty	Summer	3.48	1.23	12.2	(11.4 - 13.1)	6.00*
Ty	Winter	4.08	2.03	13.5	(12.9 - 14.1)	13.7*
Vg	Summer	5.22	1.74	11.4	(10.8 - 12.1)	10.5*
Vg	Winter	4.32	2.04	13.6	(13.1 - 14.2)	14.8*

Note: C.I. = confidence interval; significant results are denoted with an *.

interval for only two seals (Ty, Vg). The amplitude of the rhythms ranged between 1.00 and 2.89 ticks $\cdot$ min^{-1}, and higher amplitudes were observed in winter for four of five seals. All data fitted significantly to the regression model.

Seasonal Variation

All resident seals completed their moult before new seals (Table 5). The probability of this occurring by chance alone is p=0.001 (binomial distribution). Within resident and new seal groups, juveniles generally moulted first, followed by females, then males.

Patterns of daily activity (TK-H) were similar throughout the year for each seal (Table 6, Figs. 4A-12A). These patterns were also similar across seals: activity consistently peaked around midday and was lowest at night and during the early morning hours in all seasons. Seven of nine seals also exhibited significant concordance in patterns of haul out across seasons (Table 6, Figs. 4B-12B). Again, similarities among seals were evident, with most haul out generally late at night and early in the morning, and little around midday. El and Mc had variable haul out behaviour. El spent more time hauled out between 1500-0400 h but only during the summer (Fig. 6B). Mc (Fig. 8B) exhibited higher levels of haul out around midday in spring and summer and lower levels at this same time in fall and winter.

Six of seven seals exhibited significant concordance in activity patterns during breeding and non-breeding periods (Table 6, Figs. 13A-17A, 19A), Ty was the sole exception (Fig. 15A). Only three seals (Ch, Ty, Vg; Figs. 14B, 18B, 19B) showed

Table 5. Summary of observations on moult for resident and new seals.

Seal	Start of moult	End of moult
Resident		
Ja	9 March	30 March
Ba	4 April	10 May
Vc	5 April	14 May
Vg	8 April	16 May
Ty	11 April	22 May
New		
Mc	10 May	25 May
Ch	12 May	10 June
Rh	13 May	13 June
El	22 May	10 July

Table 6. Kendall's coefficient of concordance (W) test values used to determine if TK-H and ONDECK-H were concordant across seasons, breeding, and moult periods. Significantly concordant results are indicated with an *.

Seal	Season		Breeding		Moult	
	TK-H	ONDECK-H	TK-H	ONDECK-H	TK-H	ONDECK-H
Ba	0.63*	0.33*	0.44*	0.03	1.0*	0.09
Ch	0.65*	0.14*	1.0*	0.79*		
El	0.72*	0.03	0.25*	0.05		
Ja	0.22*	0.50*				
Mc	0.80*	0.04	0.72*	0.06	0.54*	0.08
Rh	0.81*	0.50*	0.84*	0.07	0.63*	0.02
Ty	0.65*	0.50*	0.07	1.0*		
Vc	0.60*	0.86*				
Vg	0.42*	0.63*	0.69*	0.20*	0.20*	0.11

Note: Empty cells indicate that no data were available.

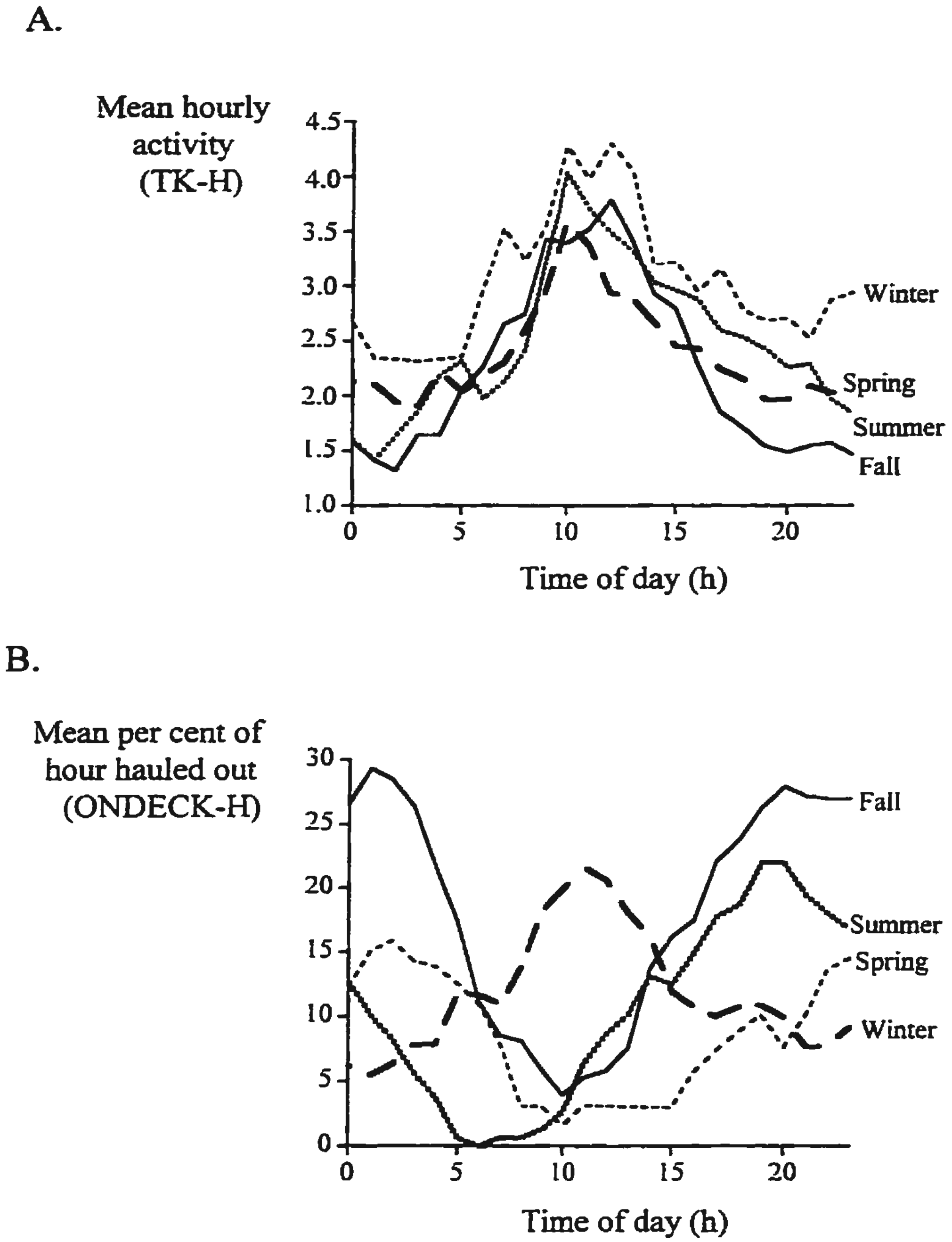


Figure 4. Daily pattern of (A) activity and (B) haul out for different seasons for Babette (Ba).

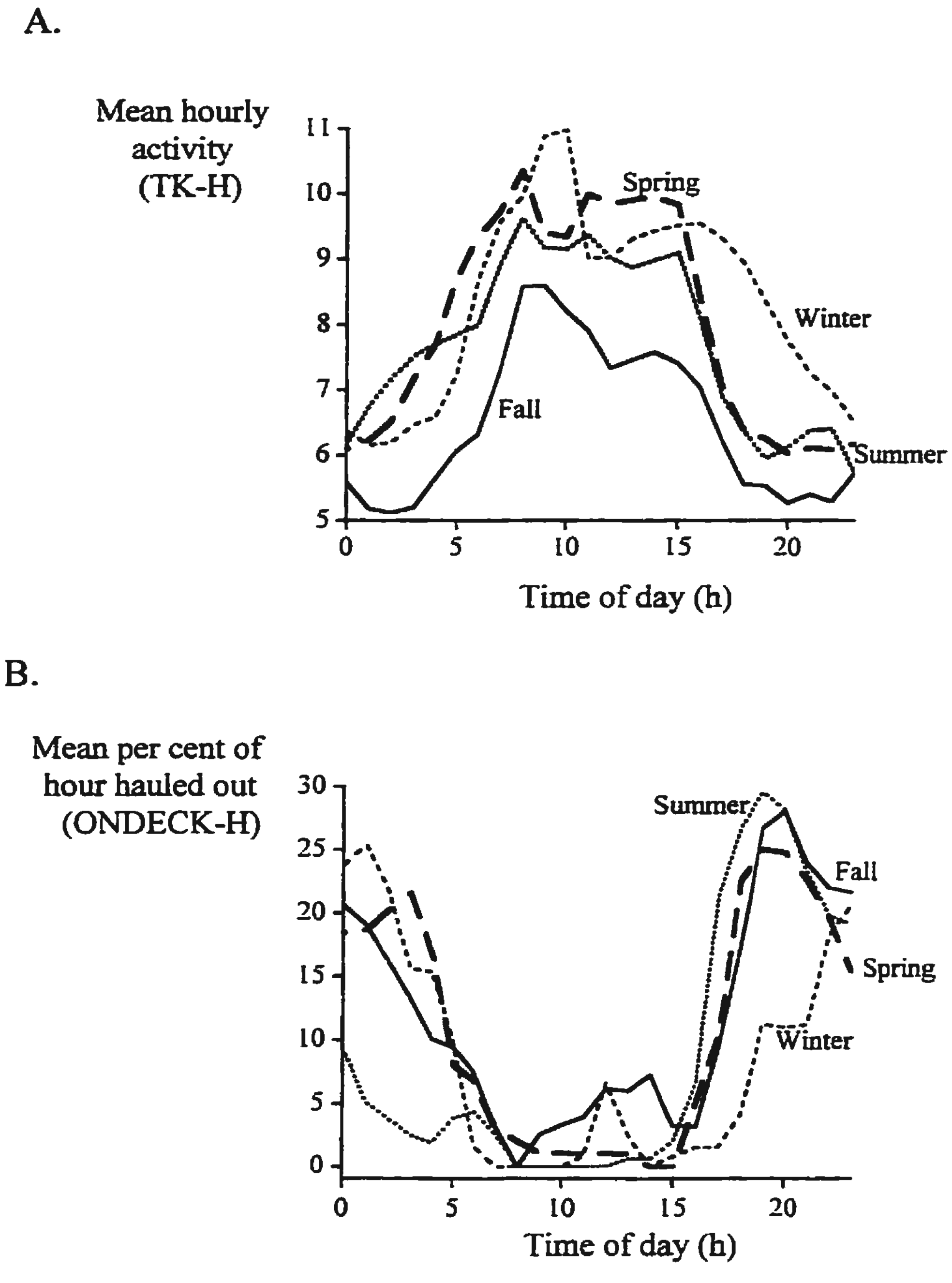


Figure 5. Daily pattern of (A) activity and (B) haul out for different seasons for Chelsea (Ch).

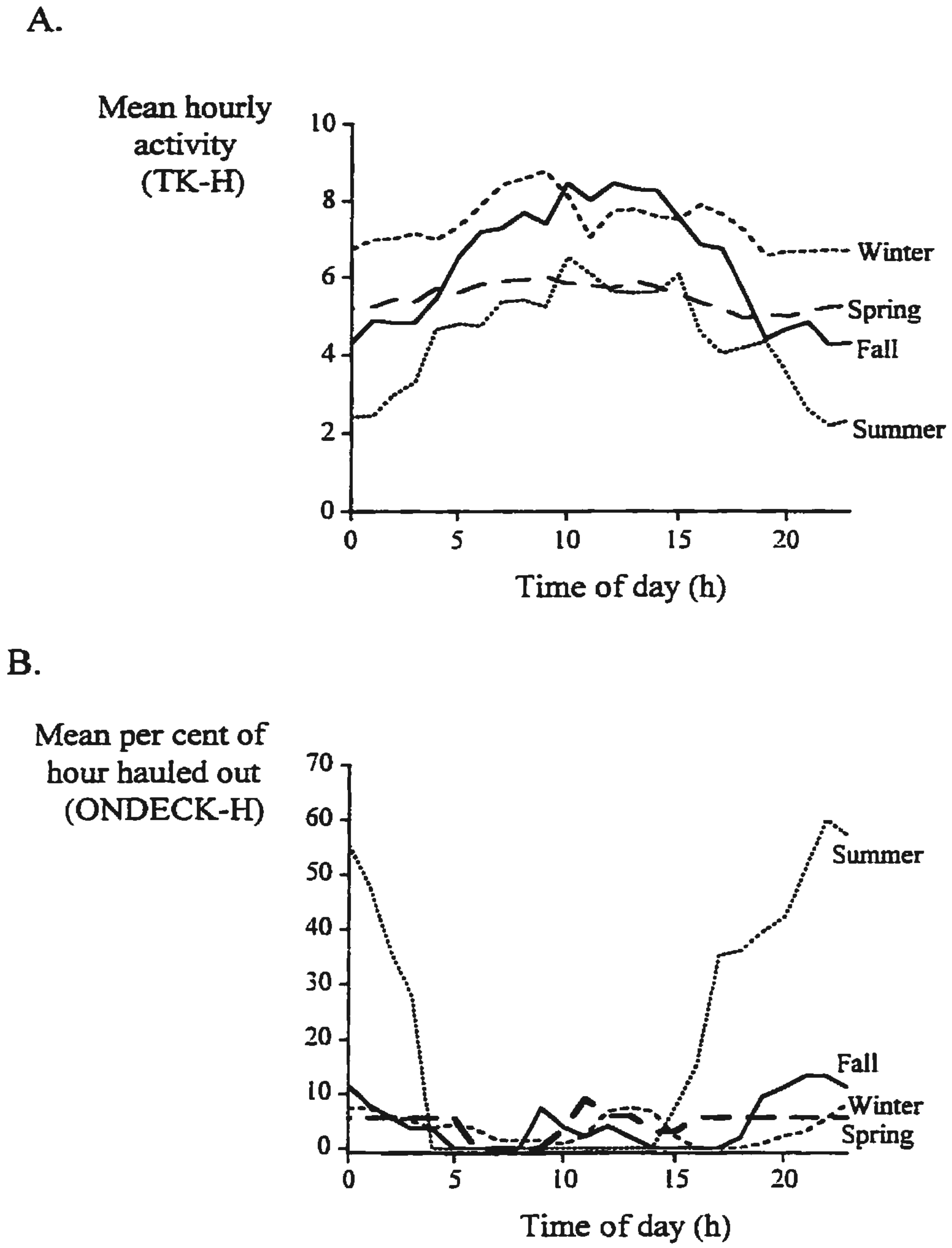


Figure 6. Daily pattern of (A) activity and (B) haul out for different seasons for Elmo (El).

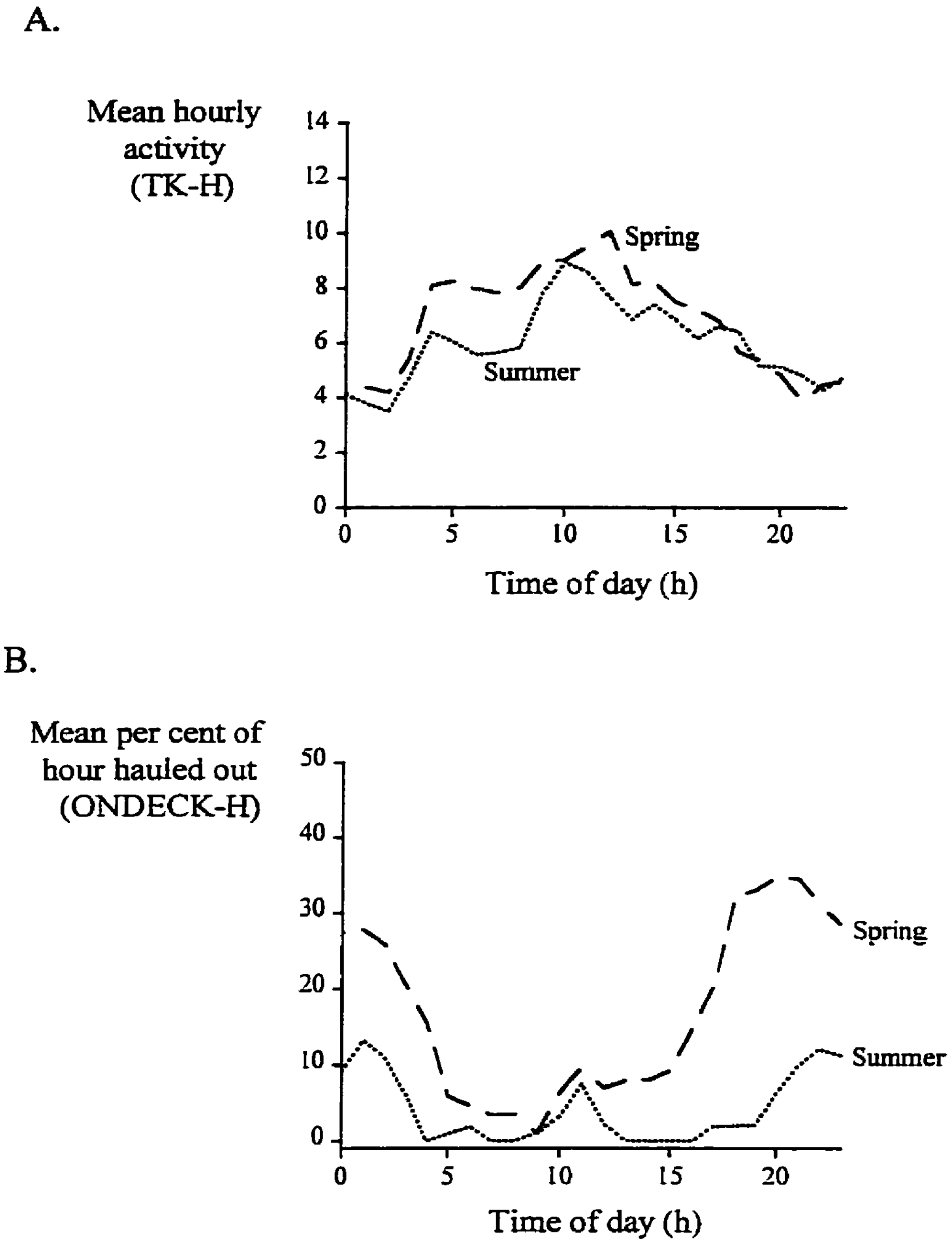
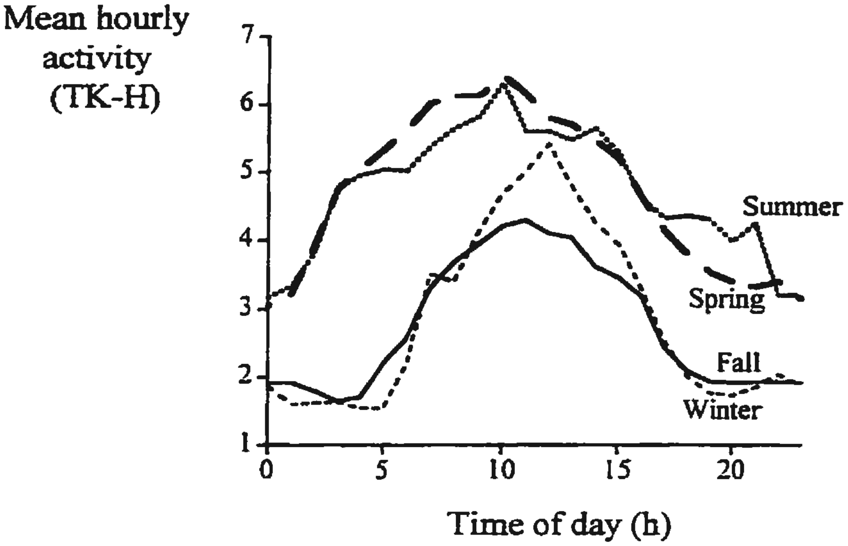


Figure 7. Daily pattern of (A) activity and (B) haul out for different seasons for Jamie (Ja).

A.



B.

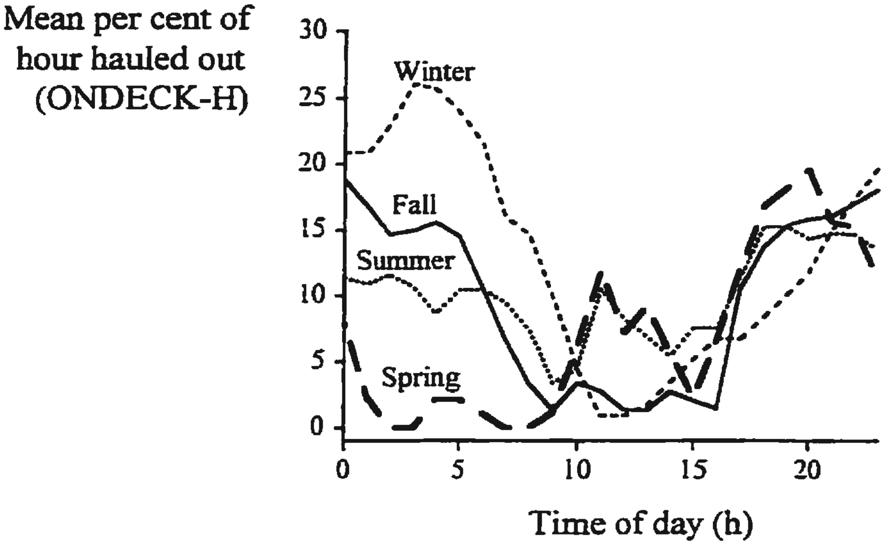
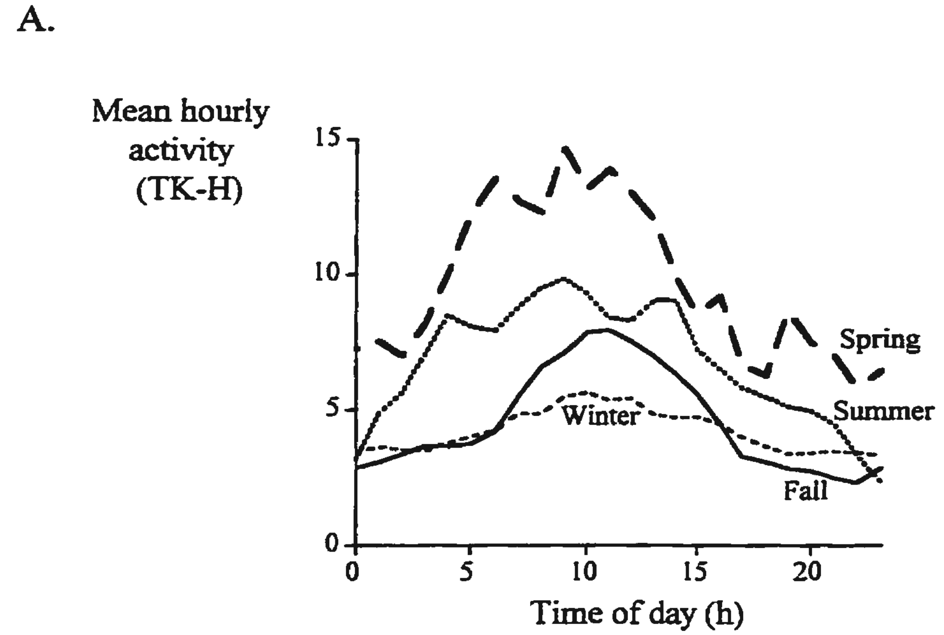


Figure 8. Daily pattern of (A) activity and (B) haul out for different seasons for Mickey (Mc).



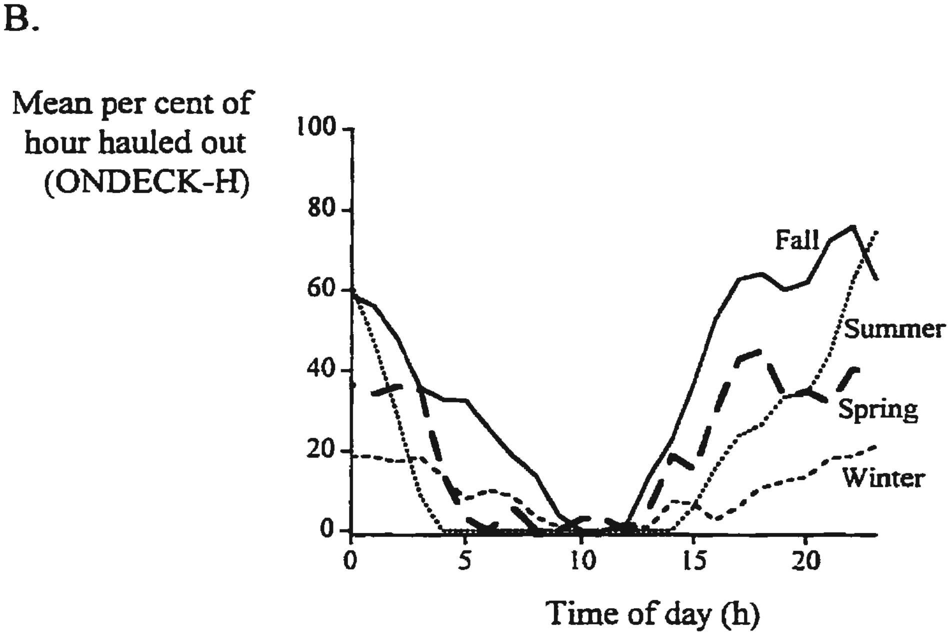


Figure 9. Daily pattern of (A) activity and (B) haul out for different seasons for Rhonda (Rh).

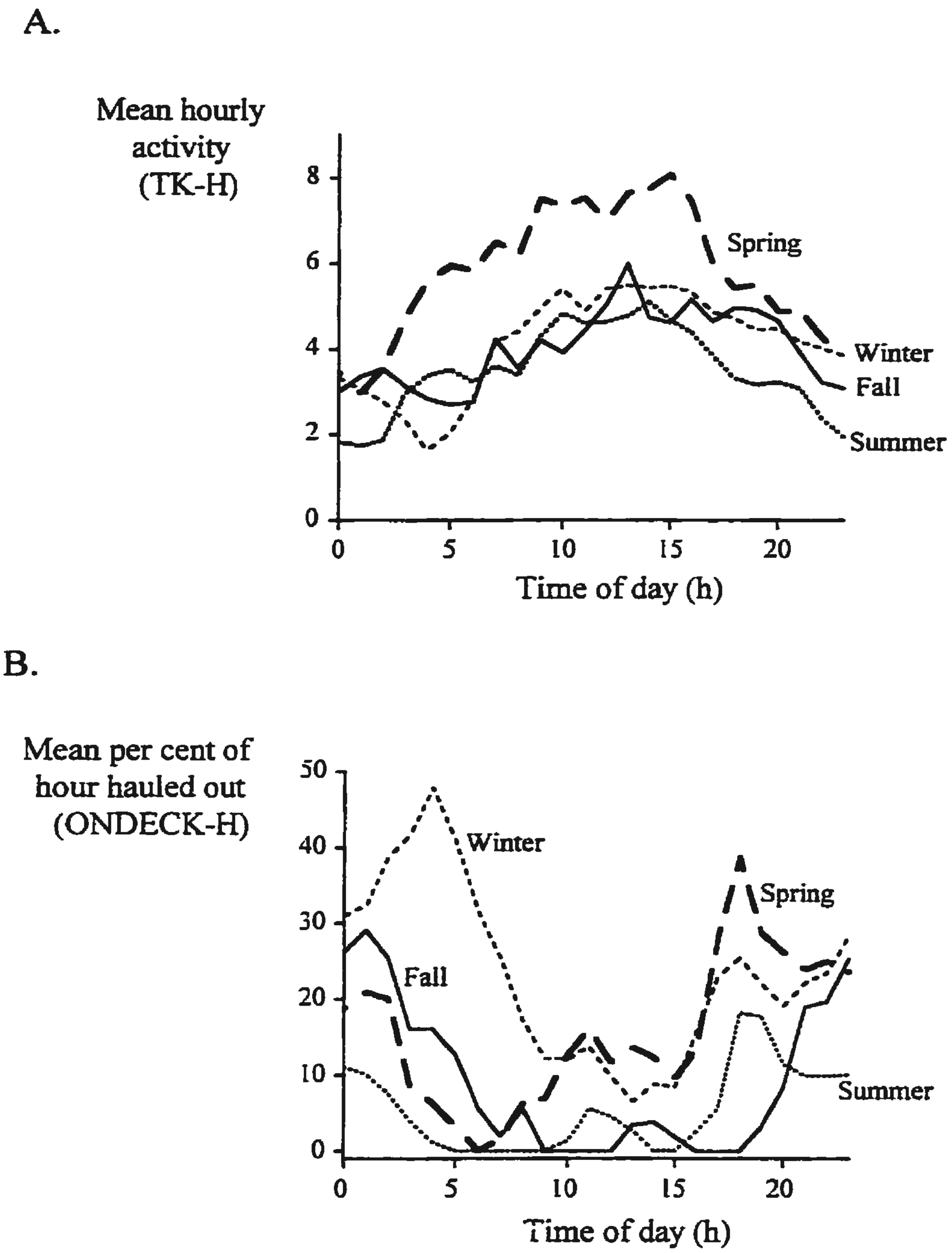


Figure 10. Daily pattern of (A) activity and (B) haul out for different seasons for Tyler (Ty).

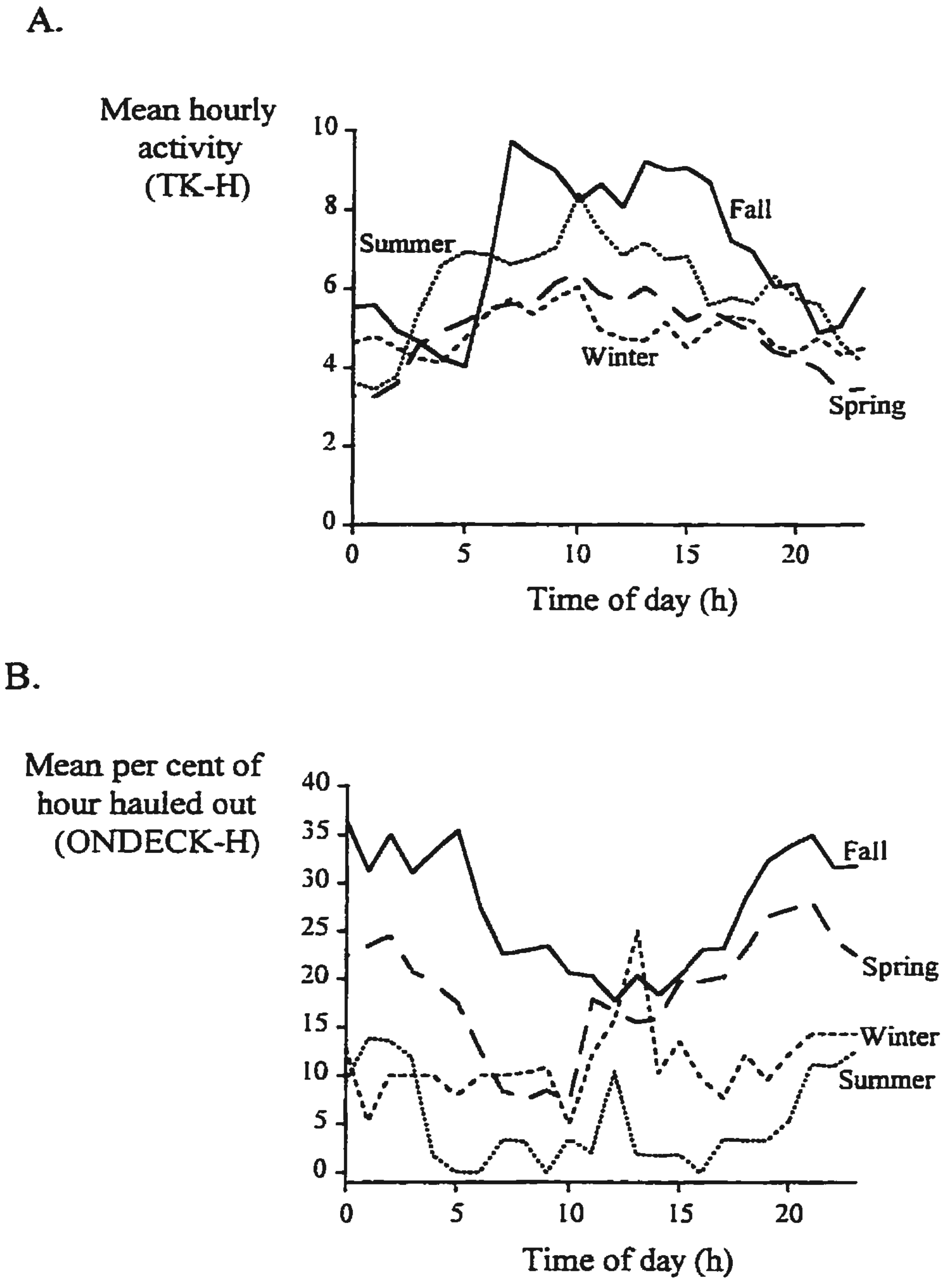
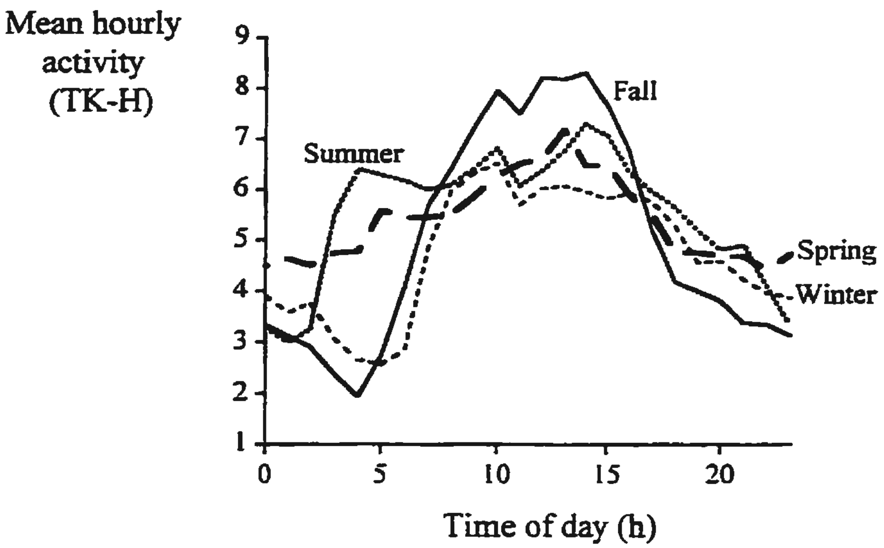


Figure 11. Daily pattern of (A) activity and (B) haul out for different seasons for Victor (Vc).

A.



B.

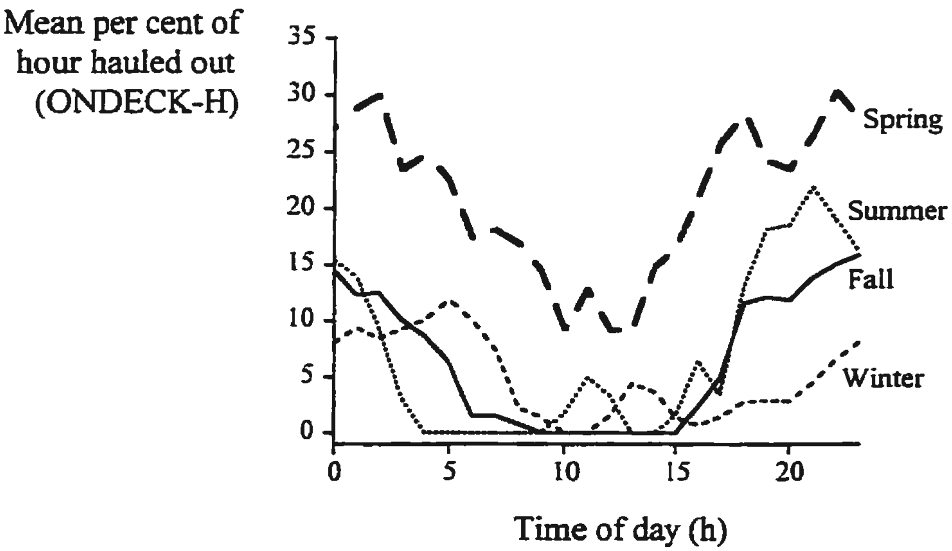


Figure 12. Daily pattern of (A) activity and (B) haul out for different seasons for Virgil (Vg).

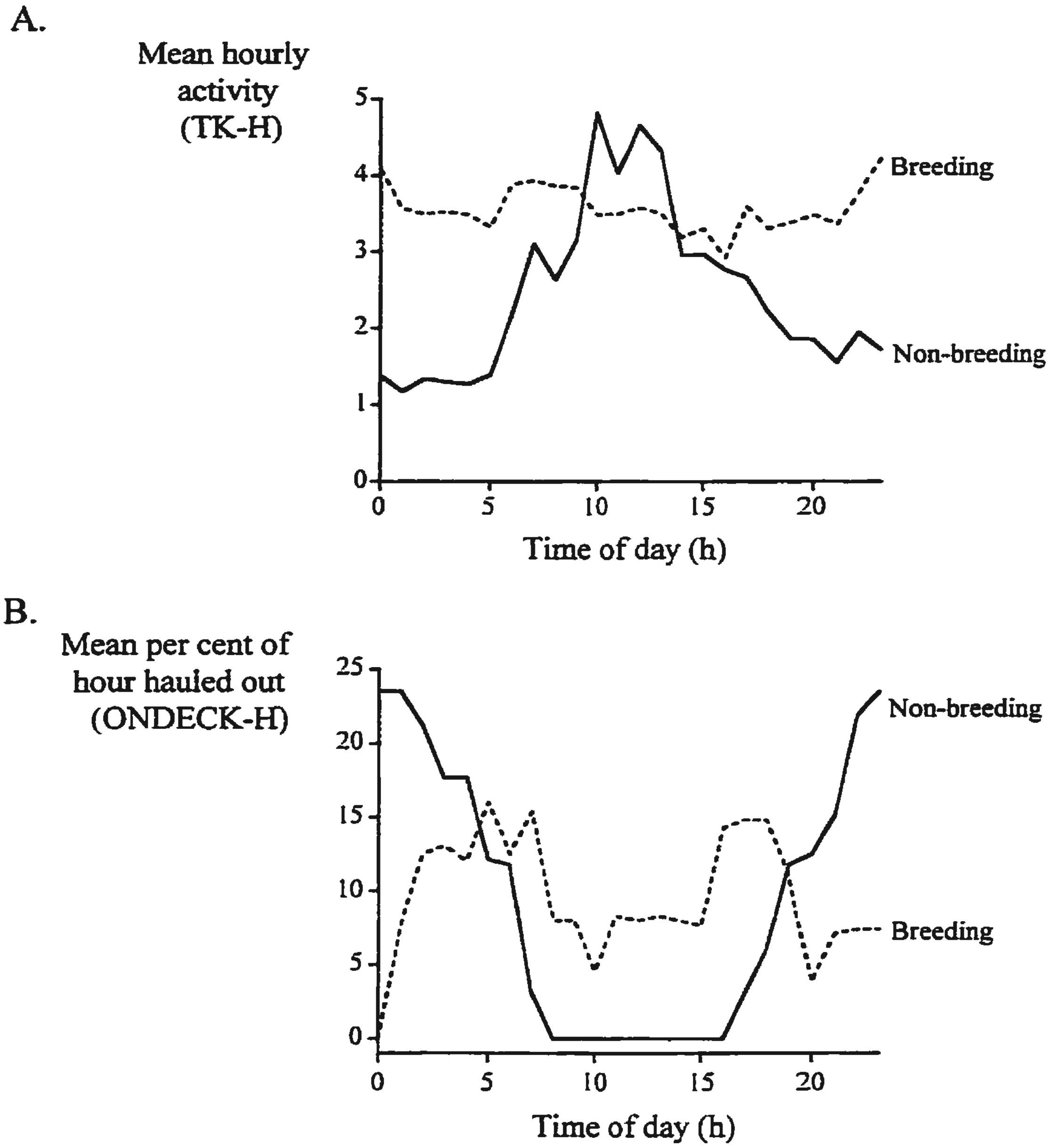


Figure 13. Daily pattern of (A) activity and (B) haul out for breeding and non-breeding periods for Babette (Ba).

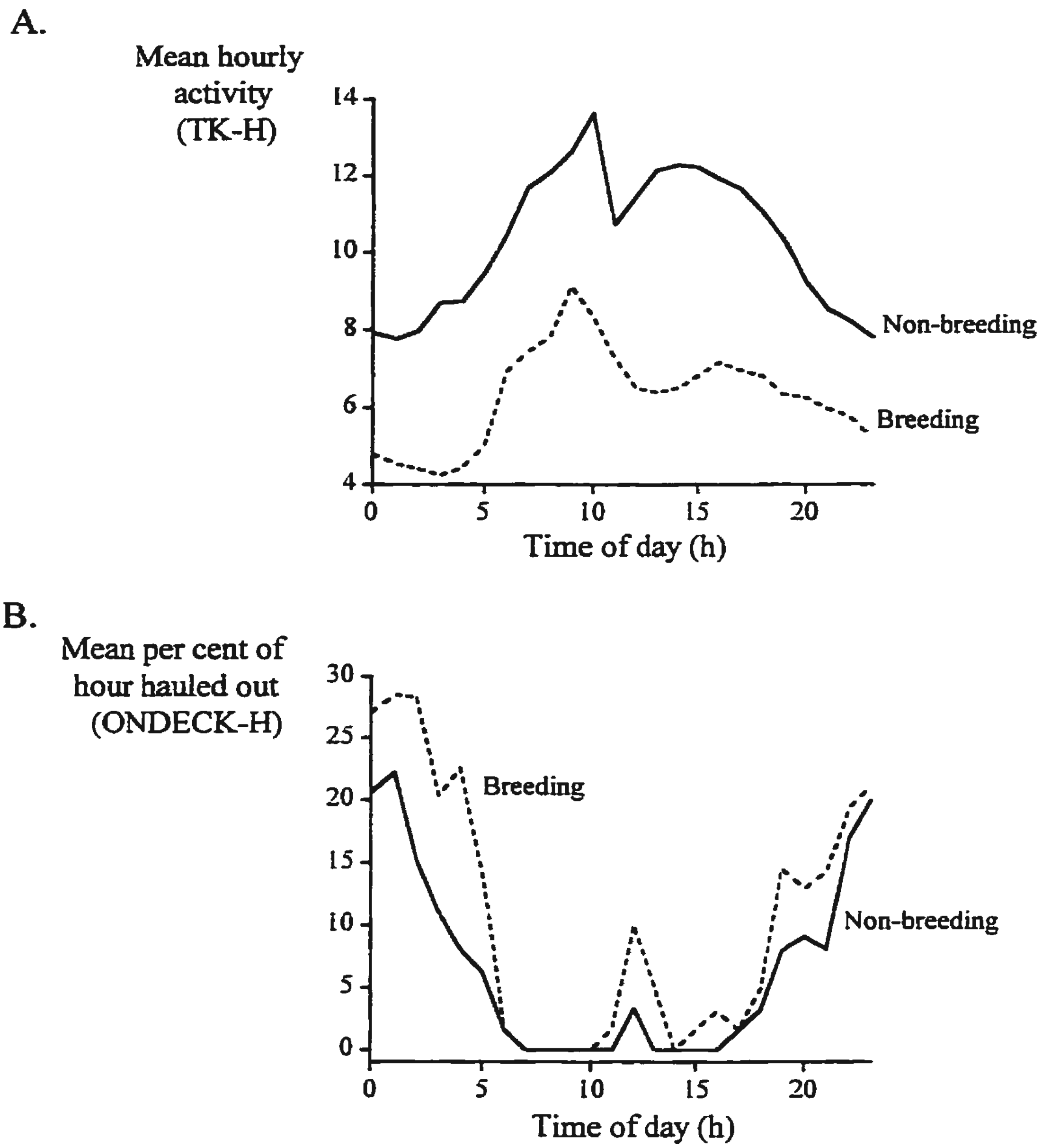


Figure 14. Daily pattern of (A) activity and (B) haul out for breeding and non-breeding periods for Chelsea (Ch).

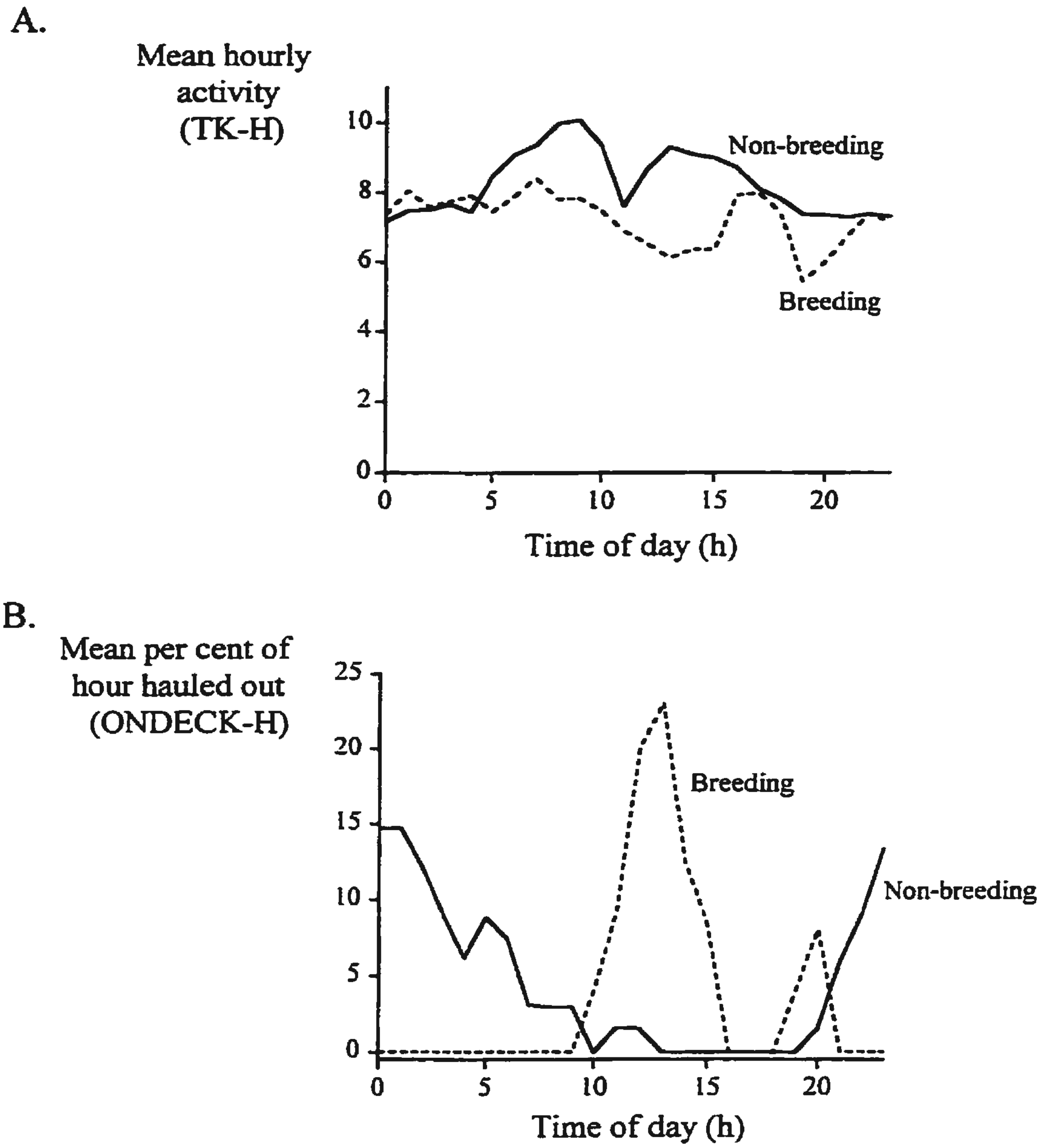


Figure 15. Daily pattern of (A) activity and (B) haul out for breeding and non-breeding periods for Elmo (El).

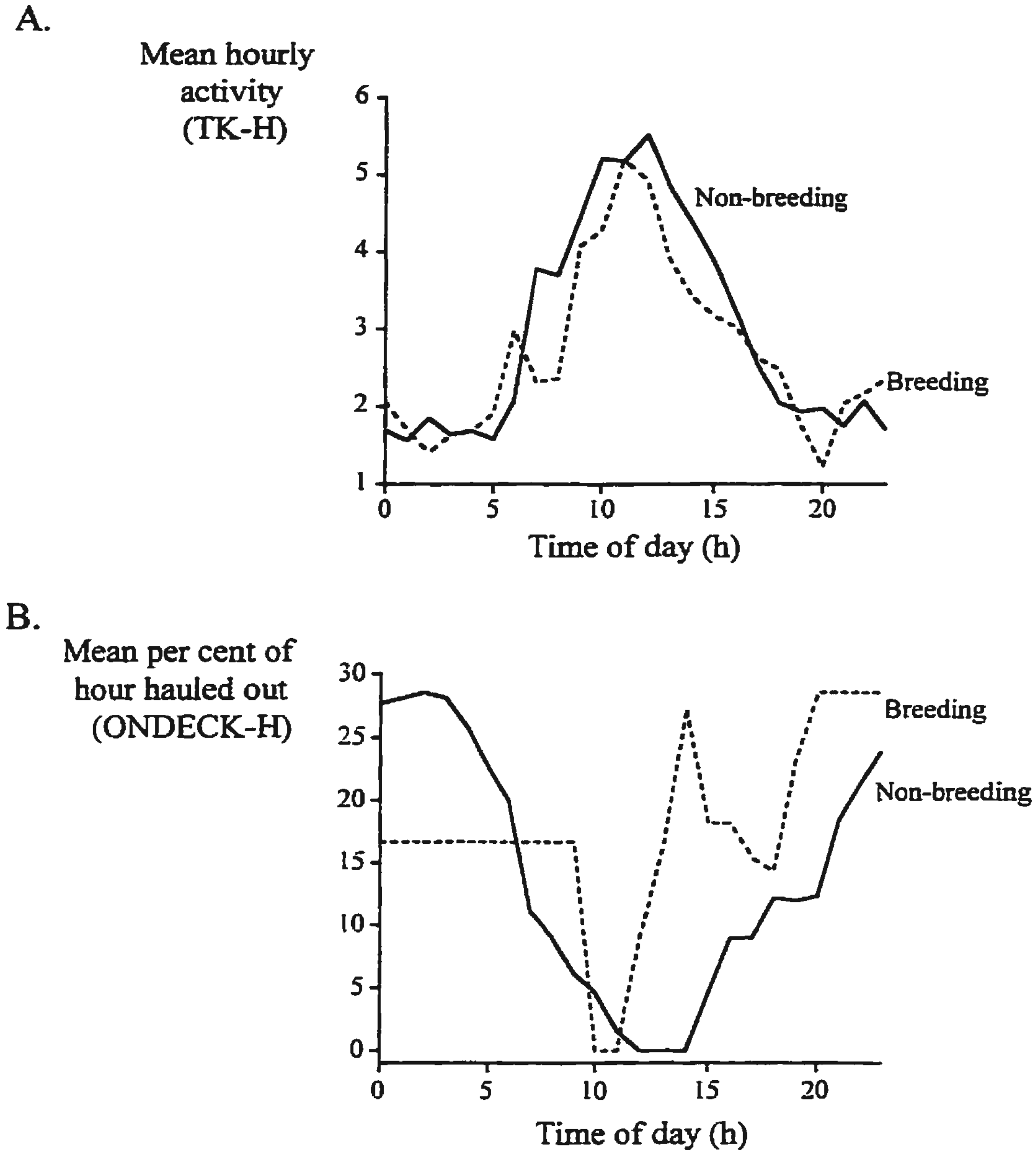


Figure 16. Daily pattern of (A) activity and (B) haul out for breeding and non-breeding periods for Mickey (Mc).

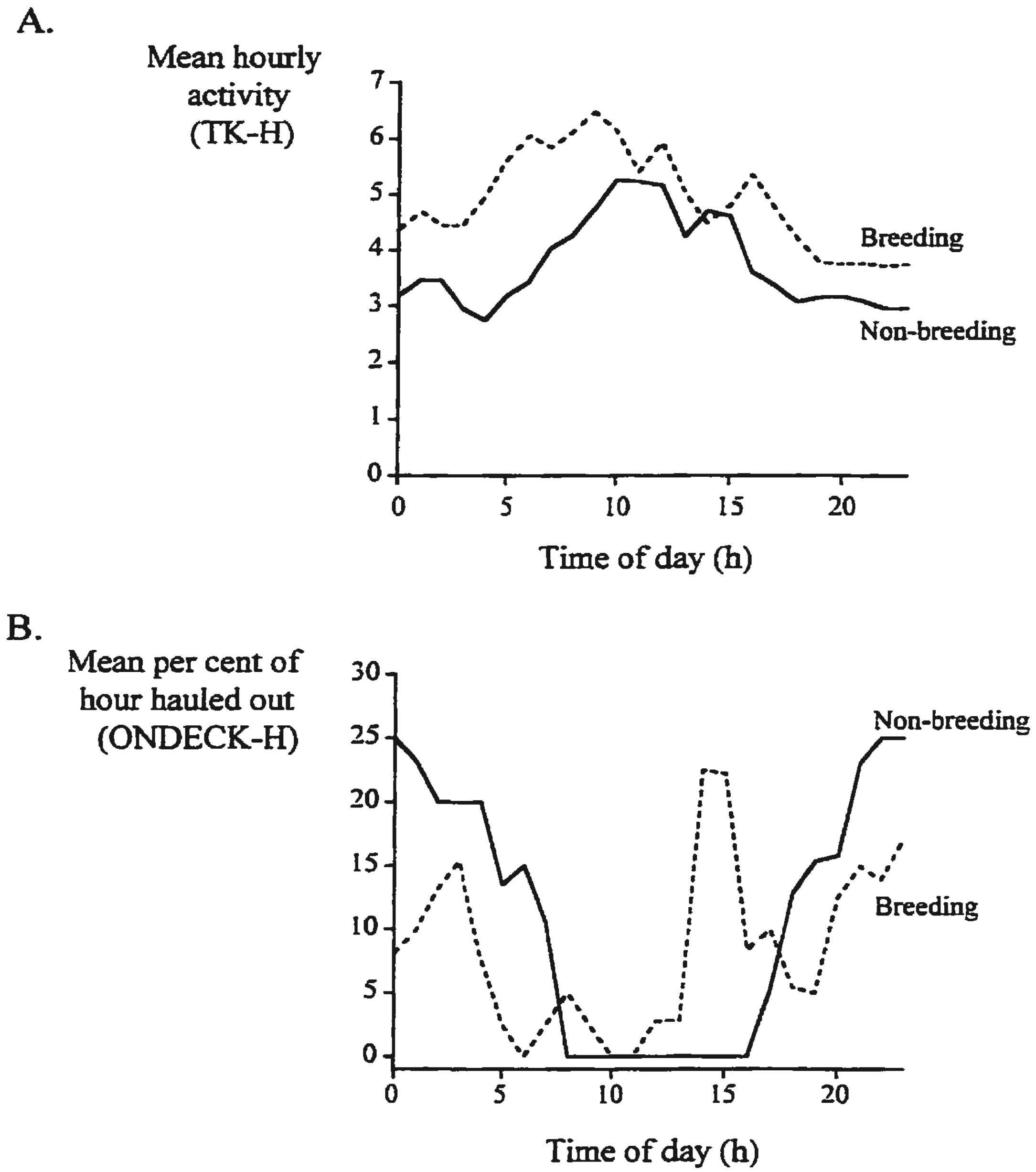


Figure 17. Daily pattern of (A) activity and (B) haul out for breeding and non-breeding periods for Rhonda (Rh).

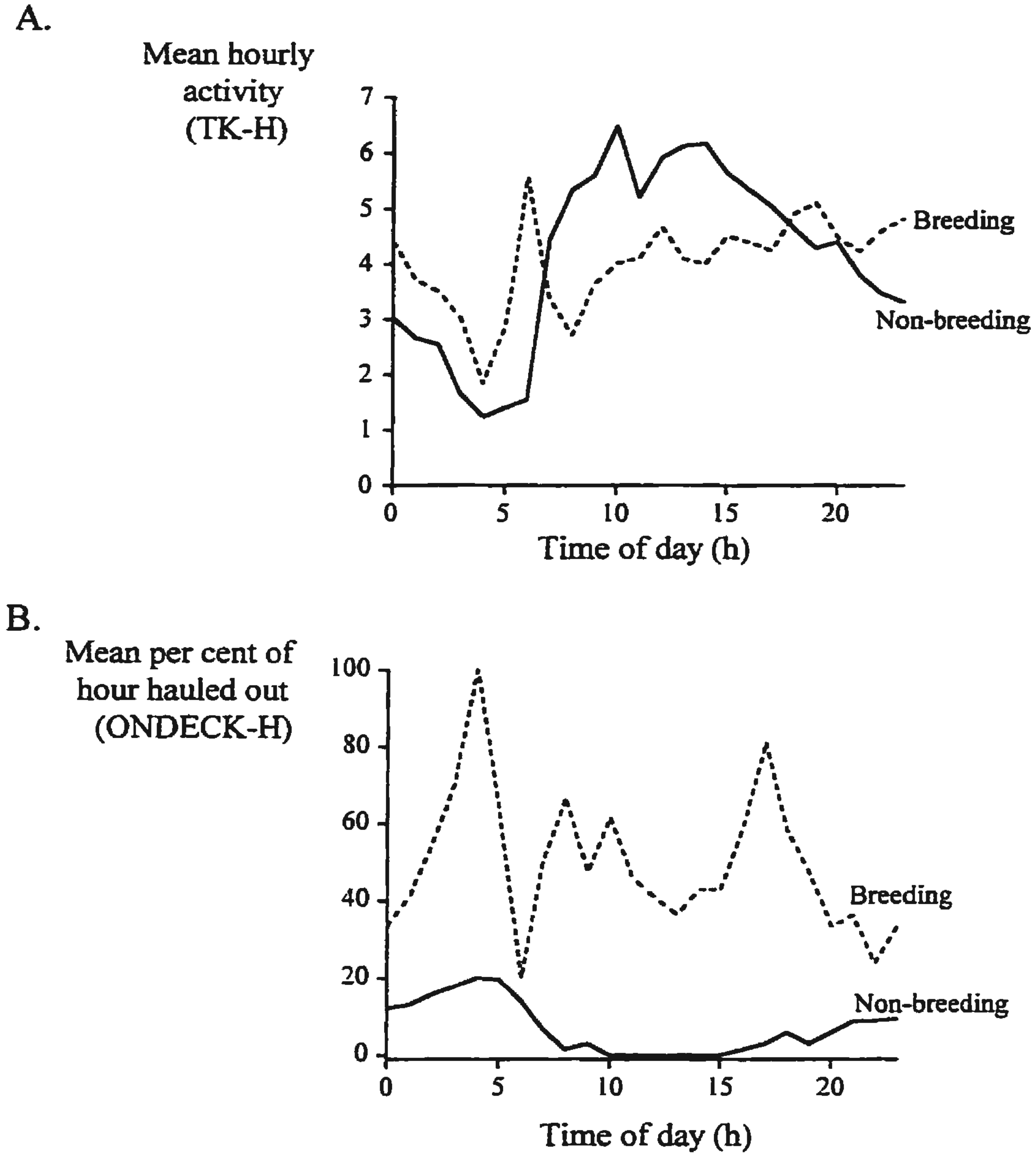


Figure 18. Daily pattern of (A) activity and (B) haul out for breeding and non-breeding periods for Tyler (Ty).

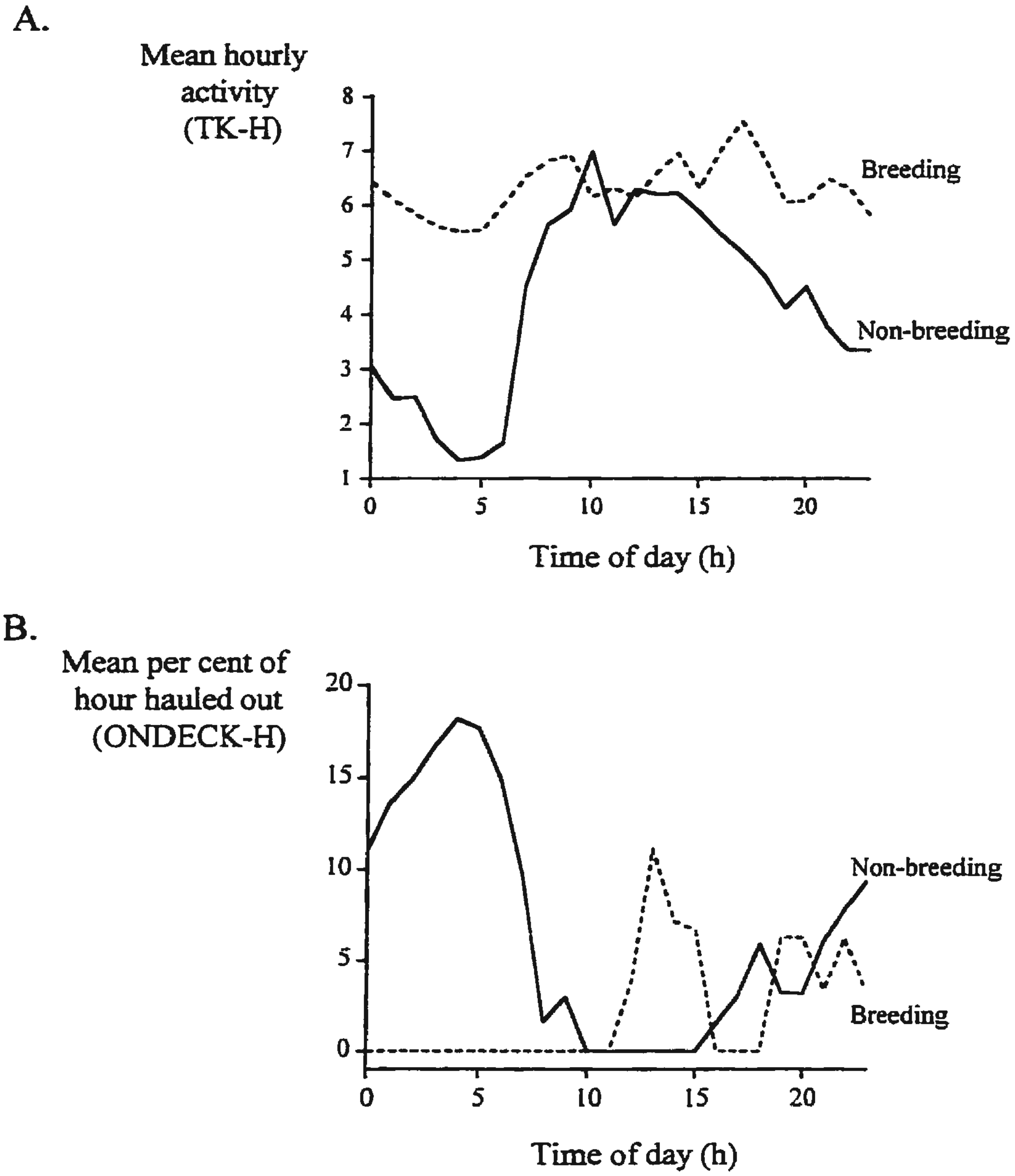


Figure 19. Daily pattern of (A) activity and (B) haul out for breeding and non-breeding periods for Virgil (Vg).

significant concordance in haul out between breeding and non-breeding. The other seals showed greater haul out levels in the afternoon during the breeding period only.

All four seals showed significant concordance in activity during moult and non-moult periods and none of the four was concordant in haul out (Table 6). Times of daily haul out varied greatly between the moult and non-moult periods (Figs. 20B-23B).

Lowest levels of activity (TIMEMIN) for all seals occurred between 2100-0200 h (Table 7), and highest levels (TIMEMAX) between 0800-1500 h (Table 8). An example of these trends for one seal (Ch) is shown in Fig. 24. There was little variation throughout the year: highest levels occurred around midday and lowest levels around midnight. However, results of Watson's F-test indicate that TIMEMIN varied seasonally within seals (except Ja; Table 7). Pooled TIMEMIN data (all seals) show that winter and spring differed significantly. TIMEMAX varied seasonally in three seals: El, 0900 h in winter and spring, and 1400 h in summer; Rh, 0800 h in spring, 1000 h in summer, and 1200 h in fall and winter; Vc, 1500 h in fall and 1100 h in winter and spring. No significant seasonal differences were found when data were pooled for all seals.

Comparisons of TIMEMIN and TIMEMAX between breeding and non-breeding periods are summarized in Table 9. Levels of activity in three of seven seals (Ba, Ty, Vg) peaked at different times during breeding and non-breeding periods: TIMEMAX occurred at night during breeding and at midday during non-breeding. TIMEMIN differed significantly in two of seven seals between breeding and non-breeding periods: El, 1700 h during breeding, and 0200 h during non-breeding; Rh, 2100 h during breeding,

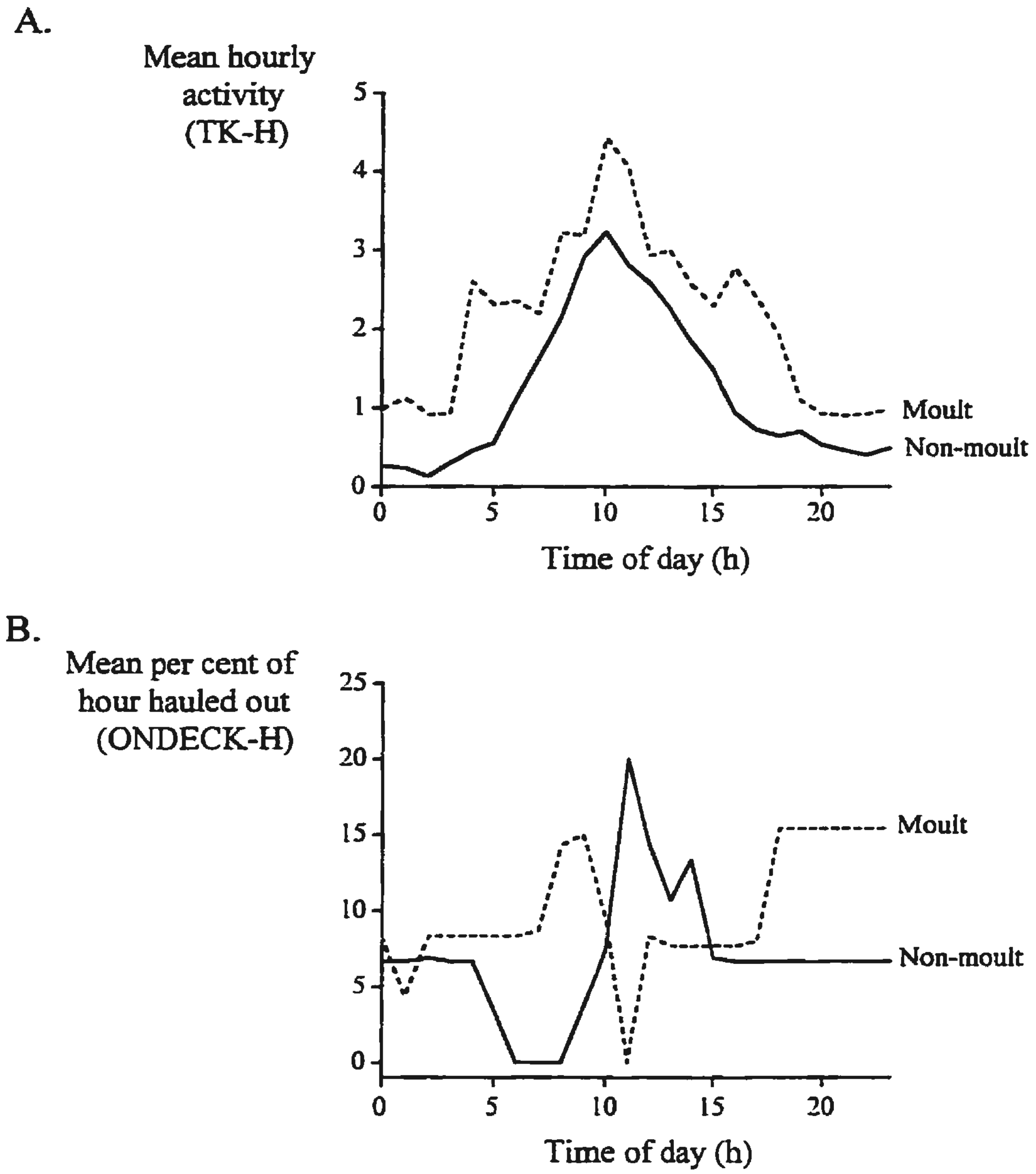


Figure 20. Daily pattern of (A) activity and (B) haul out for moult and non-moult periods for Babette (Ba).

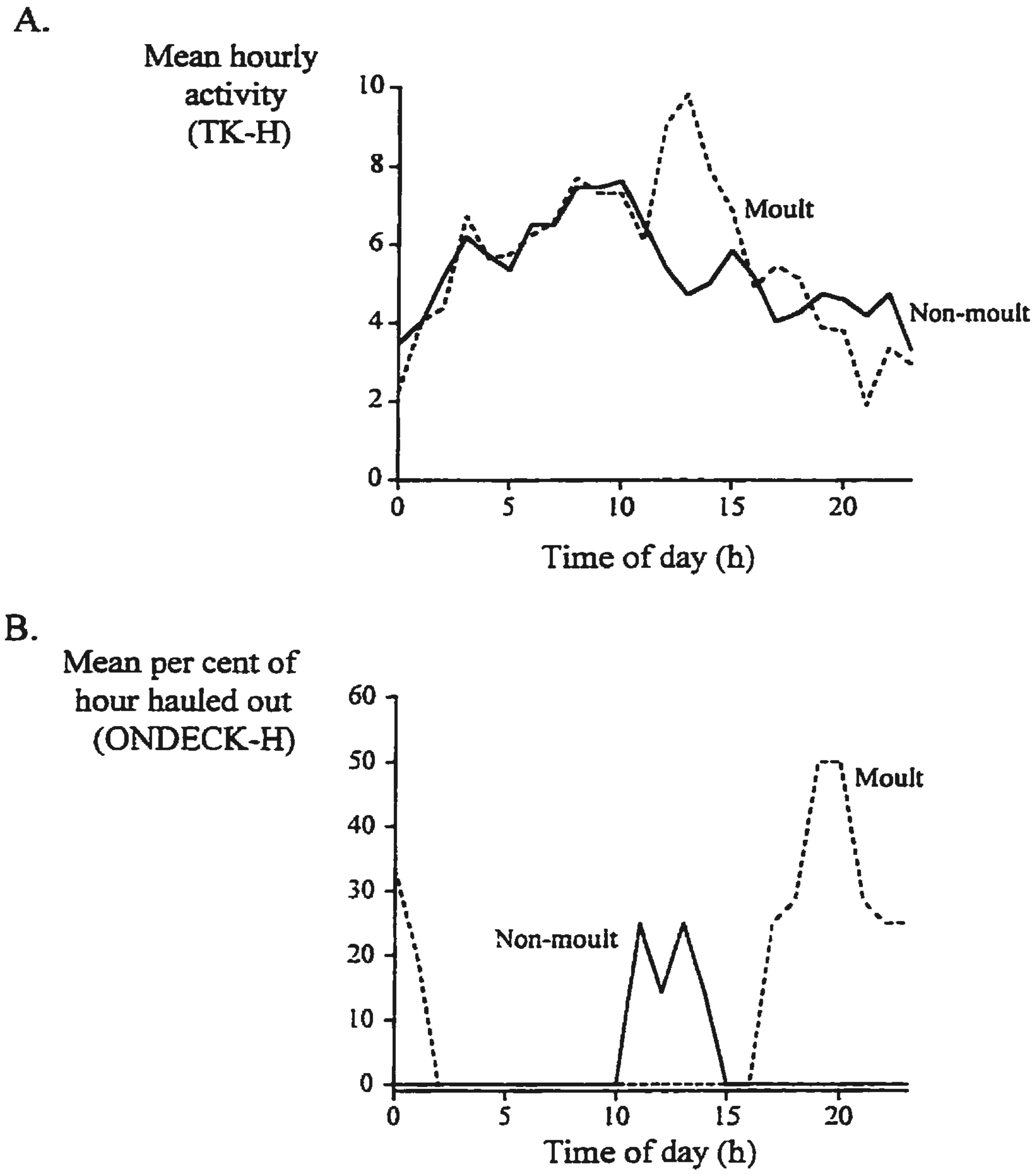


Figure 21. Daily pattern of (A) activity and (B) haul out for moult and non-moult periods for Mickey (Mc).

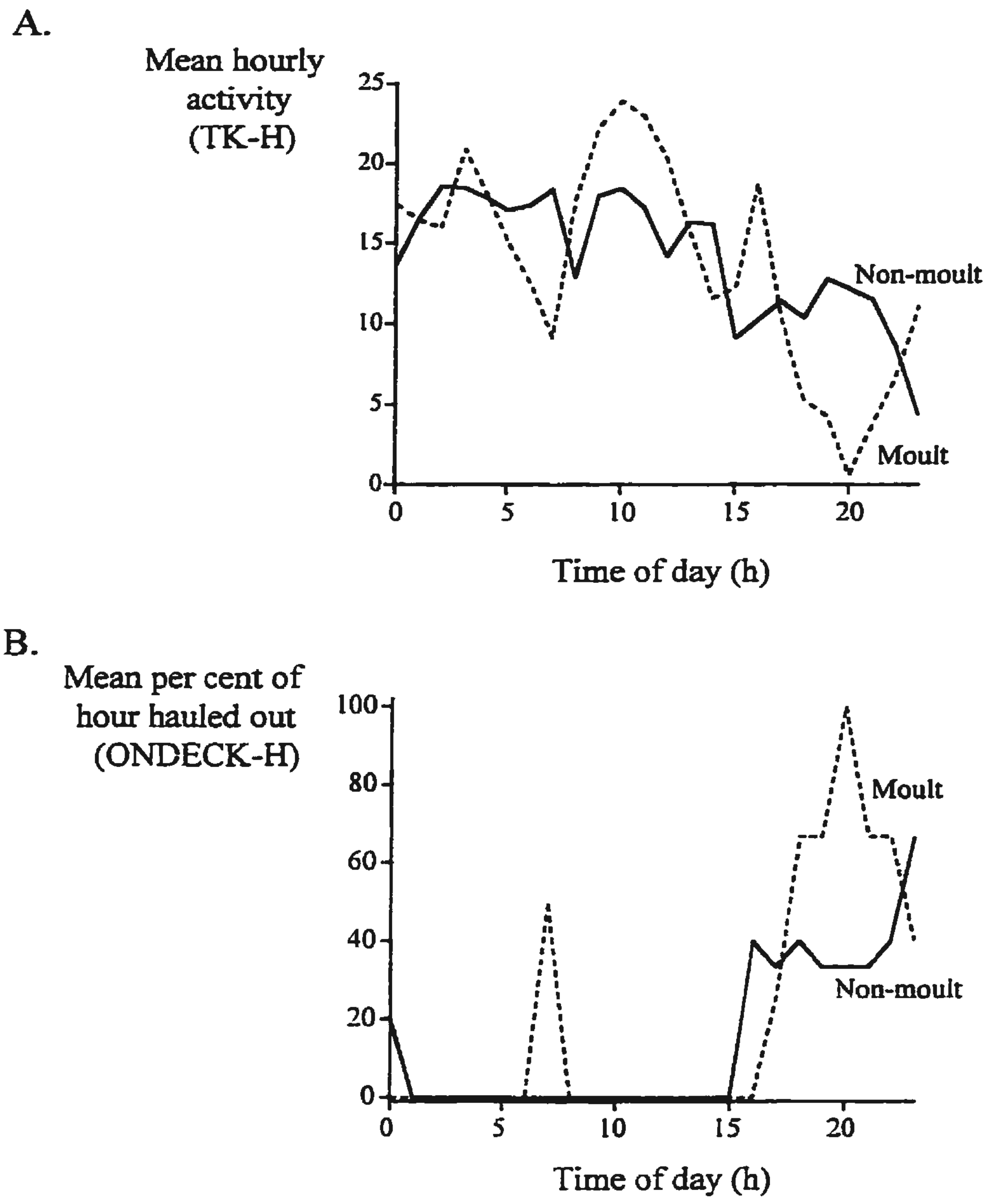


Figure 22. Daily pattern of (A) activity and (B) haul out for moult and non-moult periods for Rhonda (Rh).

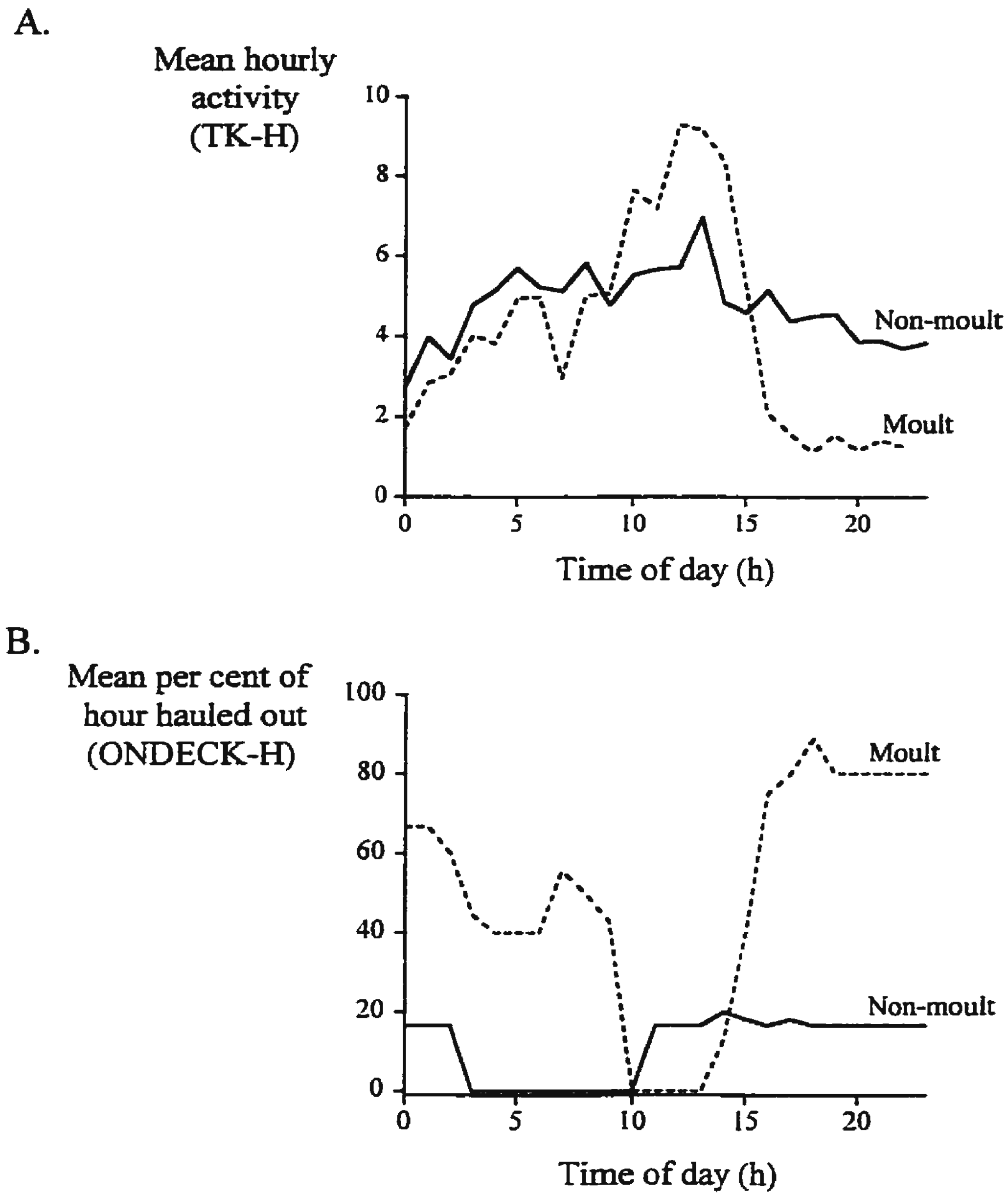


Figure 23. Daily pattern of (A) activity and (B) haul out for moult and non-moult periods for Virgil (Vg).

Table 7. Summary of mean (± s.d.) TIMEMIN and results of Watson's F-test comparing TIMEMIN across seasons for each seal and all seals (pooled data), and seals for all data.

Seal	Fall	Winter	Spring	Summer	Totals[i]
Ba[a]	0 ± 4.1	0 ± 4.3	0 ± 5.4	2 ± 4.4	0 ± 4.8
Ch[b]	23 ± 5.6	1 ± 4.2	0 ± 4.6	23 ± 4.5	0 ± 4.0
El[c]	23 ± 5.4	1 ± 5.8	21 ± 6.0	23 ± 4.1	23 ± 5.4
Ja			0 ± 4.1	1 ± 3.9	1 ± 3.9
Mc[d]	1 ± 5.4	1 ± 5.2	23 ± 5.0	23 ± 4.7	0 ± 5.7
Rh[e]	0 ± 5.6	0 ± 5.5	22 ± 5.3	0 ± 2.9	0 ± 6.1
Ty[f]	1 ± 4.1	2 ± 5.4	23 ± 4.7	23 ± 4.6	0 ± 4.5
Vc	1 ± 4.4	1 ± 11.0	0 ± 5.2	1 ± 3.7	1 ± 6.2
Vg[g]	1 ± 4.8	2 ± 4.3	0 ± 6.0	0 ± 3.3	1 ± 5.4
Totals[h]	0 ± 3.8	1 ± 5.4	23 ± 4.5	0 ± 3.1	0 ± 4.3

Note: Empty cells indicate no data were available.

[a] Significant for Ba: Summer--Fall, Winter, Spring

[b] Significant for Ch: Winter--Fall, Summer

[c] Significant for El: Winter--Fall, Spring, Summer

Table 7. (continued)

[d] Significant for Mc: Fall, Winter--Spring, Summer

[e] Significant for Rh: Spring--Fall, Winter, Summer

[f] Significant for Ty: Winter--Fall, Spring, Summer; Fall--Spring

[g] Significant for Vg: Winter--Fall, Spring, Summer; Fall--Summer

[h] Significant for season Totals: Winter--Spring

[i] Significant for seal Totals: El--Ja, Vc, Vg

Table 8. Summary of mean (± s.d.) TIMEMAX and results of Watson's F-test comparing TIMEMAX across seasons for each seal and all seals (pooled data), and seals for all data.

Seal	Fall	Winter	Spring	Summer	Totals
Ba	12 ± 4.7	13 ± 6.3	12 ± 4.5	12 ± 4.0	12 ± 5.1
Ch	12 ± 3.3	12 ± 4.5	11 ± 4.6	11 ± 4.2	12 ± 4.6
El[a]	11 ± 2.1	9 ± 4.7	9 ± 5.4	14 ± 4.8	11 ± 2.8
Ja			11 ± 5.3	12 ± 1.5	12 ± 3.9
Mc	13 ± 3.2	13 ± 3.4	11 ± 5.6	11 ± 3.7	12 ± 4.2
Rh[b]	12 ± 2.5	12 ± 4.5	8 ± 6.7	10 ± 3.8	11 ± 3.7
Ty	14 ± 6.6	12 ± 6.0	14 ± 4.6	13 ± 4.1	13 ± 5.4
Vc[c]	15 ± 5.4	11 ± 5.2	11 ± 4.8	13 ± 5.5	12 ± 5.0
Vg	13 ± 4.7	12 ± 5.1	13 ± 5.6	12 ± 4.8	13 ± 4.4
Totals	13 ± 4.6	12 ± 5.7	12 ± 4.3	12 ± 3.9	12 ± 4.5

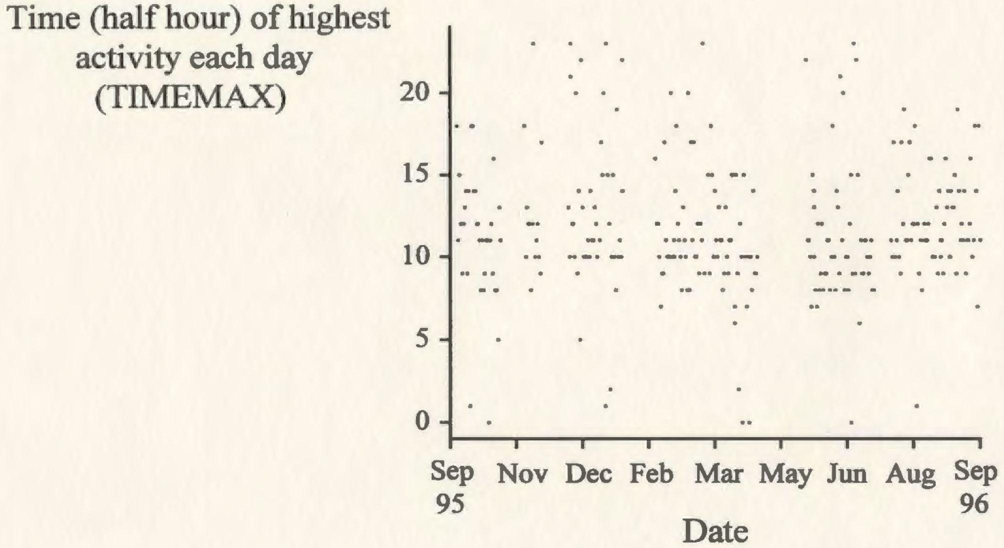
Note: Empty cells indicate no data were available.

[a] Significant for El: Summer--Fall, Winter, Spring; Fall--Winter

[b] Significant for Rh: Fall, Winter--Spring, Summer

[c] Significant for Vc: Fall--Winter, Spring

A.



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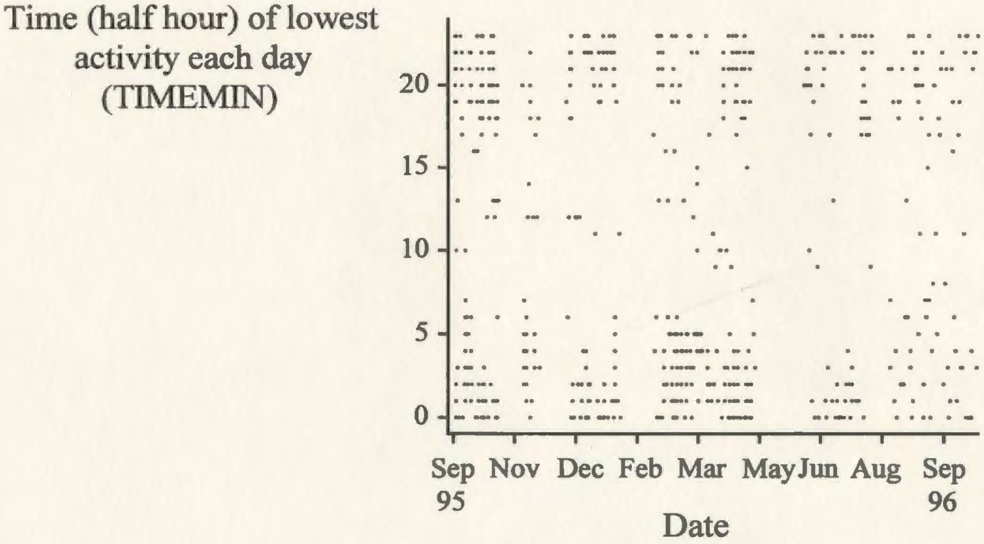

Figure 24. Time of day of (A) highest and (B) lowest levels of activity per day for Chelsea.

and 0200 h during non-breeding. Pooled data results for TIMEMIN and TIMEMAX during breeding and non-breeding did not differ significantly (Table 9).

Little variation occurred in either TIMEMIN or TIMEMAX during moult and non-moult periods (Table 10). Mc was the only exception; maximal activity occurred at 1700 h during moult and at 1000 h during the non-moult period.

The times of day when seals hauled out (TODECK) or entered the water (TOWATER) most often varied seasonally (Tables 11, 12). Seals hauled out around 1400 h during spring and 1700 h during the other three seasons (Table 11). During fall, TOWATER occurred in the early morning for most seals, and this shifted to later in the morning in winter, and to midday-late afternoon during the spring (Table 12). TOWATER were highly variable during summer.

TODECK and TOWATER varied significantly within most seals between breeding and non-breeding periods (Table 13). However, pooled data show no differences in TODECK (1800 h) and TOWATER (0900 h) during these periods.

Seals did not differ significantly in TODECK between moult and non-moult periods, and only one seal (Rh) differed significantly in TOWATER (Table 14). Seals generally hauled out and returned to the water from midday to early evening.

Levels of activity (TK-D) varied seasonally in five of nine seals (Table 15). Activity levels were significantly higher in the spring for two seals (Rh, Ty) and in the summer for one seal (Mc). TK-D were significantly lower in the fall for El and higher during this time for Vc. Pooled seasonal data for all seals show the lowest activity levels during the fall and the highest level during spring. Seasonal variation in the amount of

Table 9. Summary of mean (± s.d.) TIMEMIN and TIMEMAX during breeding (Breed.) and non-breeding (Non-breed.), and results of Watson's F-test comparing means across Breed. and Non-breed. for each seal and all seals (pooled data), and seals for all data.

	TIMEMIN			TIMEMAX		
Seal	Breed.	Non-breed.	Totals [f]	Breed.	Non-breed.	Totals [g]
Ba[a]	0 ± 5.7	0 ± 3.6	0 ± 4.2	20 ± 11.0	13 ± 4.1	17 ± 6.6
Ch	2 ± 3.9	0 ± 3.1	1 ± 3.6	11 ± 3.3	12 ± 5.6	12 ± 4.4
El[b]	17 ± 4.8	2 ± 4.2	21 ± 5.5	10 ± 5.3	12 ± 2.4	11 ± 4.5
Mc	22 ± 4.5	0 ± 4.3	23 ± 4.2	13 ± 3.9	13 ± 3.1	13± 3.6
Rh[c]	21 ± 5.4	2 ± 4.2	0 ± 4.6	11 ± 5.3	12 ± 2.4	12 ± 4.7
Ty[d]	2 ± 6.7	2 ± 3.6	2 ± 4.9	0 ± 6.3	12 ± 4.1	6 ± 5.4
Vg[e]	21 ± 5.8	3 ± 3.6	0 ± 4.8	19 ± 5.2	12 ± 3.7	16 ± 4.7
Totals	23 ± 3.9	1 ± 3.5	0 ± 4.1	14 ± 6.2	12 ± 4.2	13 ± 5.6

[a] Significant for Ba: TIMEMAX

[b] Significant for El: TIMEMIN

[c] Significant for Rh: TIMEMIN

[d] Significant for Ty: TIMEMAX

[e] Significant for Vg: TIMEMAX

[f] Significant for seal Totals (TIMEMIN): El--Ty;

[g] Significant for seal Totals(TIMEMAX): Ba--Ch, El, Mc, Rh, Ty; Ty--Ba, Ch, El, Mc, Rh, Vg; Vg--Ch, El, Mc, Rh, Ty

Table 10. Summary of mean (h ± s.d.) TIMEMIN and TIMEMAX during Moult and Non-moult and results of Watson's F-test comparing means across Moult and Non-moult for each seal and all seals (pooled data), and seals for all data.

	TIMEMIN			TIMEMAX		
Seal	Moult	Non-moult	Totals	Moult	Non-moult	Totals [b]
Ba	0 ± 3.5	1 ± 3.9	1 ± 3.3	13 ± 4.5	12 ± 1.8	12 ± 2.7
Mc[a]	20 ± 2.2	21 ± 6.1	21 ± 5.6	17 ± 2.2	10 ± 0.7	14 ± 0.9
Rh	20 ± 5.7	1 ± 3.8	23 ± 4.6	10 ± 5.7	7 ± 3.2	9 ± 4.8
Vg	1 ± 4.5	22 ± 5.5	0 ± 4.3	13 ± 2.9	12 ± 2.0	13 ± 2.8
Totals	22 ± 3.9	23 ± 5.8	23 ± 4.9	13 ± 4.5	10 ± 2.8	12 ± 3.6

[a] Significant for Mc: TIMEMAX

[b] Significant for seal Totals (TIMEMAX): Rh--Ba, Mc, Vg

Table 11. Summary of mean (h ± s.d.) TODECK and results of Watson's F-test comparing TODECK across seasons for each seal and all seals (pooled data), and seals for all data.

Seal	Fall	Winter	Spring	Summer	Totals[j]
Ba[a]	18 ± 8.2	21 ± 8.3	9 ± 4.6	14 ± 3.7	16 ± 6.3
Ch[b]	16 ± 6.5	18 ± 6.2	17 ± 6.4	18 ± 4.4	17 ± 5.0
El[c]	15 ± 7.3	15 ± 8.4	11 ± 2.0	19 ± 2.1	15 ± 4.4
Ja			14 ± 5.2	21 ± 9.9	12 ± 7.9
Mc[d]	18 ± 5.1	17 ± 6.4	12 ± 4.7	14 ± 5.7	15 ± 5.6
Rh[e]	18 ± 6.6	18 ± 7.0	15 ± 6.3	20 ± 4.2	18 ± 6.4
Ty[f]	19 ± 7.7	6 ± 10.1	16 ± 5.4	15 ± 4.8	16 ± 7.5
Vc[g]	18 ± 6.2	14 ± 4.0	14 ± 4.5	13 ± 6.4	14 ± 5.3
Vg[h]	17 ± 4.0	16 ± 8.2	13 ± 6.0	16 ± 5.1	16 ± 6.3
Totals[i]	17 ± 6.7	17 ± 7.1	14 ± 4.6	17 ± 6.7	16 ± 5.2

Note: Empty cells indicate no data were available.

[a] Significant for Ba: Summer, Spring--Fall, Winter; Spring--Summer

[b] Significant for Ch: Fall--Summer

[c] Significant for El: Spring--Summer

Table 11. (continued)

[d] Significant for Mc: Fall--Winter, Spring, Summer; Winter--Summer
[e] Significant for Rh: Spring--Summer
[f] Significant for Ty: Fall--Winter, Summer; Winter--Spring, Summer
[g] Significant for Vc: Fall--Winter, Spring, Summer
[h] Significant for Vg: Fall--Spring
[i] Significant for season Totals: Spring--Fall, Winter, Summer
[j] Significant for seal Totals: Ja--Ba, Ch, El, Mc, Rh, Ty, Vg; Rh--Vc

Table 12. Summary of mean (h ± s.d.) TOWATER and results of Watson's F-test comparing TOWATER across seasons for each seal and all seals (pooled data), and seals for all data.

Seal	Fall	Winter	Spring	Summer	Totals[j]
Ba[a]	5 ± 7.1	6 ± 4.3	13 ± 5.2	6 ± 9.8	7 ± 6.8
Ch[b]	2 ± 7.4	5 ± 5.9	6 ± 4.8	10 ± 3.7	6 ± 5.4
El[c]	6 ± 6.5	13 ± 6.8	11 ± 3.3	2 ± 4.2	8 ± 5.6
Ja			9 ± 6.4	8 ± 9.1	8 ± 7.7
Mc[d]	7 ± 5.7	10 ± 4.3	16 ± 6.4	16 ± 5.8	12 ± 5.5
Rh[e]	4 ± 5.6	5 ± 5.7	21 ± 10.3	2 ± 4.4	2 ± 8.3
Ty[f]	8 ± 5.1	10 ± 8.0	16 ± 8.5	16 ± 5.3	12 ± 6.4
Vc[g]	21 ± 7.2	14 ± 4.3	12 ± 5.2	17 ± 7.4	16 ± 5.3
Vg[h]	2 ± 6.3	11 ± 5.6	11 ± 6.7	22 ± 7.6	13 ± 6.9
Totals[i]	4 ± 5.6	9 ± 6.2	12 ± 5.4	7 ± 5.7	9 ± 5.2

Note: Empty cells indicate no data were available.

[a] Significant for Ba: Fall, Winter--Spring, Summer

[b] Significant for Ch: Fall--Spring; Summer--Fall, Winter, Spring

Table 12. (continued)

[c] Significant for El: Winter--Fall, Summer; Spring--Summer
[d] Significant for Mc: Fall-- Spring, Summer; Winter--Summer
[e] Significant for Rh: Winter-- Spring
[f] Significant for Ty: Fall, Winter --Spring, Summer
[g] Significant for Vc: Fall--Winter, Spring; Spring--Summer
[h] Significant for Vg: Fall, Summer--Winter, Spring
[i] Significant for season Totals: All seasons significantly different except Winter and Summer
[j] Significant for seal Totals: Ba, Ch, El, Ja--Mc, Rh, Ty, Vc, Vg; Rh--all seals

Table 13. Summary of mean (h ± s.d.) TODECK and TOWATER during breeding (Breed.) and non-breeding (Non-breed.), and results of Watson's F-test comparing means across Breed. and Non-breed. for each seal and all seals (pooled data), and seals for all data.

	TODECK			TOWATER		
Seal	Breeding	Non-breeding	Totals[g]	Breeding	Non-breeding	Totals[h]
Ba[a]	19 ± 3.6	6 ± 6.6	1 ± 5.3	7 ± 5.5	6 ± 2.2	7 ± 4.5
Ch[b]	21 ± 3.5	16 ± 6.0	19 ± 4.5	5 ± 6.2	7 ± 6.7	6 ± 5.8
El[c]	13 ± 3.2	20 ± 6.9	17 ± 4.3	16 ± 3.4	8 ± 4.2	12 ± 4.0
Mc	16 ± 2.7	18 ± 3.7	17 ± 2.9	9 ± 3.4	13 ± 2.4	11± 3.1
Rh[d]	19 ± 6.0	17 ± 5.9	18 ± 5.6	20 ± 6.0	8 ± 3.2	15 ± 4.9
Ty[e]	3 ± 7.5	18 ± 7.3	22 ± 6.8	6 ± 9.5	10 ± 6.0	8 ± 7.4
Vg[f]	15 ± 3.9	21 ± 7.3	18 ± 5.7	16 ± 4.1	9 ± 6.1	13 ± 5.6
Totals	18 ± 3.8	18 ± 5.2	18 ± 4.3	9 ± 5.6	9 ± 4.7	9 ± 5.0

[a] Significant for Ba: TODECK

[b] Significant for Ch: TODECK

[c] Significant for El: TODECK and TOWATER

[d] Significant for Rh: TOWATER

[e] Significant for Ty: TODECK

[f] Significant for Vg: TOWATER

[g] Significant for seal Totals (TODECK): Ba--Ch, El, Mc, Rh, Vg;

[h] Significant for seal Totals (TOWATER): Ba, Ch, Ty--El, Mc, Rh, Vg

Table 14. Summary of mean (h ± s.d.) TODECK and TOWATER during Moult and Non-moult and results of Watson's F-test comparing means across Moult and Non-moult for each seal and all seals (pooled data), and seals for all data.

		TODECK			TOWATER	
Seal	Moult	Non-moult	Totals[b]	Moult	Non-moult	Totals[c]
Ba	8 ± 5.9	10 ± 1.7	9 ± 3.5	8 ± 3.0	12 ± 3.4	10 ± 2.9
Mc	16 ± 3.3	11 ± 0.3	13 ± 2.7	12 ± 2.2	15 ± 0.6	14 ± 0.9
Rh[a]	15 ± 4.0	18 ± 3.5	17 ± 3.6	17 ± 4.5	5 ± 3.8	23 ± 4.1
Vg	14 ± 3.3	12 ± 1.9	13 ± 2.4	7 ± 4.2	9 ± 2.6	8 ± 3.6
Totals	13 ± 3.9	12 ± 2.6	12 ± 3.7	8 ± 3.4	10 ± 2.9	9 ± 2.7

[a] Significant for Rh: TOWATER

[b] Significant for seal Totals (TODECK): Ba--Mc, Rh, Vg

[c] Significant for seal Totals (TOWATER): Rh--Ba, Mc, Vg

Table 15. Summary of mean (± s.d.) TK-D and results of one-way ANOVA comparing TK-D across seasons for each seal and all seals (pooled data), and seals for all data.

Seal	Fall	Winter	Spring	Summer	Totals[g]
Ba	2.5 ± 3.01	3.1 ± 1.47	1.9 ± 1.05	2.5 ± 2.05	2.4 ± 2.16
Ch	6.6 ± 3.37	8.1 ± 3.15	7.9 ± 2.33	7.8 ± 1.51	7.5 ± 2.74
El[a]	6.7 ± 1.93	7.0 ± 1.27	5.4 ± 0.89	3.6 ± 0.76	6.2 ± 1.79
Ja			6.9 ± 1.52	5.9 ± 1.41	6.4 ± 1.53
Mc[b]	2.7 ± 0.79	3.2 ± 0.85	4.9 ± 1.24	5.4 ± 1.01	3.7 ± 1.45
Rh[c]	4.5 ± 1.47	4.0 ± 1.43	9.3 ± 5.34	6.7 ± 2.44	5.7 ± 3.36
Ty[d]	4.2 ± 0.91	4.1 ± 0.85	6.5 ± 2.38	3.5 ± 1.22	4.5 ± 1.72
Vc[e]	6.6 ± 1.48	4.6 ± 0.63	5.1 ± 0.92	6.0 ± 1.73	5.6 ± 1.40
Vg	4.9 ± 2.15	4.7 ± 1.03	5.8 ± 1.23	5.5 ± 0.65	5.1 ± 1.51
Totals[f]	4.6 ± 2.83	5.0 ± 2.34	5.7 ± 2.87	5.2 ± 2.45	5.1 ± 2.65

Note: Empty cells indicate no data were available.

[a] Significant for El: Winter>Summer, Spring; Fall>Summer

[b] Significant for Mc: Summer>Winter, Fall; Spring>Winter, Fall

[c] Significant for Rh: Spring>Fall, Winter; Summer>Winter

Table 15. (continued)

[d] Significant for Ty: Spring>Fall, Winter, Summer
[e] Significant for Vc: Fall>Spring, Winter
[f] Significant for season Totals: Winter, Spring, Summer>Fall; Spring>Winter, Summer
[g] Significant for seal Totals: all seals significantly different except, Rh/Vc and El/Ja

time hauled out (ONDECK-D) occurred in three of nine seals: El spent more time hauled out in summer; Rh spent more time hauled out in fall than winter; Ty spent more time hauled out in winter than summer (Table 16). Pooled seasonal data for all seals did not vary significantly.

Higher levels of activity (TK-D) occurred during the breeding period in two of seven seals (Ba, Vg) and one seal (Ch) showed the opposite result (Table 17). ONDECK-D varied significantly between breeding and non-breeding periods in one seal (Ty; Table 17).

Significantly higher levels of activity (TK-D) occurred during the moult period for one seal (Ba; Table 18) and one seal significantly spent more time hauled out during the moult (Vg; Table 18). Pooled data show that ONDECK-D was significantly greater during moult than the non-moult period.

Individuality, Sex, and Captivity Status Groups

Most activity (TK-D, TIMEMIN) and haul out measures (ONDECK-D, TODECK, TOWATER) differed among individuals (Tables 7, 8, 11, 12, 15, 16) for all data. TK-D varied the most (Table 15), and TIMEMAX varied the least (Table 8). However, TIMEMAX did differ significantly among individuals (Ba, Ty, Vg) during breeding (Table 9).

Females spent significantly more time hauled out (ONDECK-D) than males, but sex did not account for significant variation in any other variables (Table 19). Seals of the new group had significantly higher levels of activity than the resident group but captivity

Table 16. Summary of mean (± s.d.) ONDECK-D and results of one-way ANOVA comparing ONDECK-D across seasons for each seal and all seals (pooled data), and seals for all data.

Seal	Fall	Winter	Spring	Summer	Totals[d]
Ba	19.8 ± 24.21	12.2 ± 21.16	16.4 ± 30.09	14.1 ± 23.28	16.1 ± 24.81
Ch	14.0 ± 16.60	9.4 ± 14.05	11.7 ± 18.89	11.2 ± 13.06	11.7 ± 15.49
El[a]	2.3 ± 4.19	5.3 ± 10.92	5.5 ± 9.83	42.8 ± 28.69	10.1 ± 19.09
Ja			16.5 ± 18.75	6.9 ± 9.40	14.2 ± 19.76
Mc	12.9 ± 25.13	10.7 ± 22.76	5.9 ± 9.03	3.9 ± 9.25	9.3 ± 19.99
Rh[b]	44.0 ± 28.06	18.4 ± 27.37	26.3 ± 25.17	22.7 ± 16.11	25.9 ± 26.02
Ty[c]	9.6 ± 13.19	36.4 ± 36.56	21.0 ± 23.65	7.6 ± 13.04	21.7 ± 28.75
Vc	24.4 ± 32.83	13.9 ± 17.21	20.6 ± 25.01	5.1 ± 6.59	17.2 ± 24.23
Vg	10.7 ± 23.12	8.3 ± 12.26	20.6 ± 22.77	4.7 ± 7.71	11.3 ± 18.99
Totals	16.0 ± 23.88	15.1 ± 24.66	16.2 ± 22.28	11.9 ± 17.82	13.8 ± 20.55

Note: Empty cells indicate no data were available.

[a] Significant for El: Summer> Fall, Winter, Spring

[b] Significant for Rh: Fall>Winter

[c] Significant for Ty: Winter>Summer

[d] Significant for seal Totals: Rh>Ba, Ch, El, Ja, Mc, Vc, Vg; Ty>Ch, El, Ja, Mc, Vg; Vc>Mc

Table 17. Summary of mean (± s.d.) TK-D and ONDECK-D during breeding (Breed.) and non-breeding (Non-breed.) and results of one- way ANOVA comparing means across Breed. and Non-breed. for each seal and all seals (pooled data), and seals for all data.

	TK-D			ONDECK-D		
Seal	Breed.	Non-breed.	Totals	Breed.	Non-breed.	Totals[e]
Ba[a]	3.6 ± 0.32	2.1 ± 0.84	2.7 ± 0.95	6.0 ± 3.01	18.1 ± 32.13	12.3 ± 22.61
Ch[b]	6.3 ± 2.35	9.9 ± 2.91	8.1 ± 3.14	12.3 ± 11.14	7.5 ± 12.56	9.4 ± 14.04
El	6.9 ± 0.07	7.8 ± 1.39	7.5 ± 1.23	5.1 ± 2.48	7.2 ± 14.33	6.7 ± 13.13
Mc	3.0 ± 0.03	3.2 ± 1.01	3.2 ± 1.00	0.0 ± 0.00	14.4 ± 6.13	13.2 ± 28.16
Rh	4.5 ± 1.77	3.4 ± 1.27	3.8 ± 1.48	17.4 ± 2.45	14.7 ± 7.84	19.2 ± 27.84
Ty[c]	3.5 ± 1.12	4.3 ± 0.83	3.9 ± 0.97	46.8 ± 4.23	7.1 ± 1.67	21.9 ± 31.49
Vg[d]	6.3 ± 0.90	4.3 ± 0.74	4.9 ± 1.17	4.0 ± 1.22	9.4 ± 1.56	7.2 ± 12.73
Totals	5.1 ± 1.86	5.4 ± 2.99	5.3 ± 2.59	17.3 ± 24.72	10.9 ± 21.03	13.4 ± 22.68

[a] Significant for Ba (TK-D): Breed.>Non-breed.

[b] Significant for Ch (TK-D): Non-breed.>Breed.

[c] Significant for Ty (ONDECK-D): Breed.>Non-breed.

[d] Significant for Vg (TK-D): Breed.>Non-breed.

[e] Significant for seal Totals (TK-D): Ch>Ba, Mc, Rh, Ty; El> Ba, Mc, Rh, Ty

Table 18. Summary of mean (± s.d.) TK-D and ONDECK-D during Moult and Non-moult and results of one-way ANOVA comparing means across Moult and Non-moult for each seal and all seals (pooled data), and seals for all data.

	TK-D			ONDECK-D		
Seal	Moult	Non-moult	Totals[d]	Moult	Non-moult	Totals[e]
Ba[a]	2.2 ± 1.71	1.2 ± 0.31	1.6 ± 0.65	10.1 ± 2.31	14.1 ± 2.63	12.1 ± 2.68
Mc	5.7 ± 0.09	5.3 ± 0.51	5.5 ± 0.32	29.1 ± 2.56	10.5 ± 2.33	19.8 ± 5.69
Rh	12.4 ± 2.23	14.2 ± 2.82	13.3 ± 2.64	51.7 ± 1.45	31.3 ± 3.78	41.5 ± 6.98
Vg[b]	4.7 ± 1.80	4.3 ± 1.35	4.5 ± 1.68	71.6 ± 13.24	23.5 ± 3.86	47.5 ± 16.52
Totals[c]	6.3 ± 1.54	6.3 ± 1.38	6.2 ± 2.14	40.8 ± 10.37	20.0 ± 5.67	30.2 ± 11.44

[a] Significant for Ba (TK-D): Moult>Non-moult
[b] Significant for Vg (ONDECK-D): Moult>Non-moult
[c] Significant for Breed/Non-breed Totals (ONDECK-D): Moult>Non-Moult
[d] Significant for seal Totals (TK-D): Rh>Ba, Mc, Vg;
[e] Significant for seal Totals (ONDECK-D): Rh>Ba, Mc; Vg>Ba, Mc

Table 19. Sex and captivity status accounted for significant variation in haul out and activity, respectively.

	Test	Sex	Captivity Status
Activity			
TK-D	ANOVA		new>residents
TIMEMIN	Watson's F		
TIMEMAX	Watson's F		
Haul out			
ONDECK-D	ANOVA	females>males	
TODECK	Watson's F		
TOWATER	Watson's F		
HAULOUTS	Kruskal-Wallis		

Note: Empty cells indicate insignificant results and text indicates significant results.

status did not account for significant variation in any other variables. Resident and new seals were similar in frequency of haul outs per day (Table 20). Both groups had no haul outs per day for approximately sixty per cent of the study period and one haul out per day for approximately thirty per cent of the study period.

Prey Type and Food Intake

Prey type and amount of food eaten did not significantly influence the activity (TK-D) of any seals. However, nighttime activity (0000-0600 h) was significantly lower in two seals that were fasted, and daytime activity (1000-1600 h) was significantly lower in one of two seals during this period (Table 21).

Table 20. Relative frequency of days with 0 to 5+ haul outs per day (HAULOUTS) for individuals, resident/new seals, and all seals, as percentage of total study days.

	HAULOUTS					
Seal	0	1	2	3	4	5+
Resident						
Ba	67.3	24.6	3.8	1.9	0.4	2.0
Ja	61.9	31.0	4.4	2.7	0	0
Ty	41.5	34.2	14.5	5.7	2.6	1.5
Vc	59.5	31.5	5.4	3.4	0.7	0
Vg	65.9	30.1	1.8	1.3	0.9	0
Mean	59.7	29.8	5.8	2.9	1.0	0.8
New						
Ch	55.1	35.1	7.7	1.1	1.1	0
El	73.6	20.7	3.6	1.4	0.7	0
Mc	73.7	22.0	3.4	0.8	0	0
Rh	32.9	32.3	14.9	11.8	5.0	3.1
Mean	59.2	28.3	7.2	3.2	1.5	0.6
Mean (all seals)	59.5	29.1	6.5	3.0	1.2	0.8

Table 21. Mean TK-HH (± s.d.) from 0000-0600 h and 1000-1600 h during fasting and regular feeding periods. Significant Kruskal-Wallis analysis results indicated by an *.

	0000-0600 h		1000-1600 h	
Seal	Fast	Fed	Fast	Fed
Ch	*6.1 ± 2.21	8.2 ± 1.74	*8.0 ± 3.64	10.0 ± 3.96
Mc	*1.4 ± 0.76	2.3 ± 0.95	3.3 ± 1.68	3.5 ± 1.44

Discussion

Most activity and haul out measures varied seasonally for each seal in this study. However, individual variation in these behaviours often made it difficult to formulate general patterns for the entire group. For instance, of the five seals with significant seasonal variation in daily activity, two exhibited highest levels during spring, two during fall, and the other had its highest level during summer. Also, all measures, except time of day of maximal activity, varied significantly among individual seals. Individual differences in activity and haul out have been noted in several pinniped species (Cameron 1970; Arnold and Trillmich 1985; Thompson and Rothery 1987; Thompson et al. 1989; Rosen 1995). These differences can be as distinct as some harbour seals preferring to haul out in the day and others at night (Yochem et al. 1987). It also appears that free-ranging harp seals exhibit high levels of individuality in both haul out and diving behaviour (G. Stenson, unpubl. data). These findings demonstrate the importance of considering the degree of variance due to individuality when discussing the behaviour of a population.

Although individual variation persisted throughout the study, certain behavioural trends common to all individuals became clearer during key annual cycle events. As expected, seals spent significantly more time hauled out during moult (41 %) than during the non-moult period (20%), and the rest of the year (14 %). This increase in amount of time spent hauled out during moult has been noted in other captive and free-ranging pinnipeds (Laws 1953; McLaren 1958; Backhouse 1960; Nel 1968; Mansfield 1970; Burns and Frost 1979; Smith and Hammill 1981; Kelly and Quakenbush 1990; Rosen 1995; Grellier et al. 1996). Free-ranging harp seals haul out in large aggregations during

April and May to undergo their annual moult (Sergeant 1965; 1991). Pinnipeds need to haul out, especially during moult, to elevate skin temperatures to a level high enough (17-19°C) for epidermal mitosis and new hair growth (Feltz and Fay 1966). When seals are immersed in water, the skin temperature is always very close to water temperature (Irving and Hart 1957; Hart and Irving 1959; McGinnis 1975). In this study, water temperatures did not exceed 15°C, so haul out was advantageous for growth of new hair. Haul out also exposed the seals to solar radiation that not only heats the skin, but is also used to synthesize vitamin D that is heavily used during hair growth (McLaren 1958; Feltz and Fay 1966; Øritsland 1974; Fay 1982). Harp seals in this study, hauled out significantly earlier in the day during both moult (1300 h) and spring (1400 h), than during the rest of the year (1700 h). Similar shifts in haul out have been noted in ringed seals (Kelly and Quankenbush 1990) and harbour seals (Thompson et al. 1989). During the spring, time of day of haul out coincided with highest solar radiation levels (see Chapter 4).

Contrary to my initial predictions, activity did not decrease during moult despite increased haul out; in fact, activity was highest during the spring (which encompassed moult for most seals). Total activity may not have decreased as predicted because the aquatic activity component may have increased. During moult, seals were often observed quickly going in and out of the tank as they attempted to gain a position on the haul out ramp that was usually occupied by other moulting seals. These haul out attempts may have increased measures of aquatic activity and masked the influence of increased haul out on total activity.

Another key annual cycle event in this study was breeding. During this time, only two of seven seals, the adult female Babette and the adult male Virgil, had significantly higher activity. These were the two seals most often observed involved in copulatory behaviour. Blood samples taken from all adult male seals as part of another study indicated that testosterone increased during the breeding period for three of the four males (El, Ty, Vg; A. Serrano, pers. comm.) and that Vg had the highest testosterone level. Increased testosterone concentrations have been observed in other seasonal breeders (Lincoln and Short 1980), including pinnipeds (Sinha et al. 1977; Griffiths 1984; Bester 1990; Bartsh et al. 1992). El (a new seal) may not have increased activity during breeding, despite high testosterone levels, because of the apparent stress from captivity. El exhibited stereotypic behaviour throughout the study and was never observed performing aquatic displays or interactions. Similarly, Mc (a new seal) may not have increased activity during breeding because of stress due to captivity or because he may not have been sexually mature (i.e., very low testosterone levels and no vocalizations during breeding; A. Serrano, pers. comm.). Ty spent significantly more time hauled out during breeding than non-breeding, even though he was observed attempting to copulate with Ba in the water. I cannot think of a plausible explanation for this increased haul out during breeding, as copulation out of the water is rare (Stirling 1975; Merdsoy et al. 1978), and it was not observed in this study. Activity levels in other phocids are known to peak during the breeding season as both aquatic displays and interactions occur (Bartsh et al. 1992; Rosen 1995). Higher activity during breeding may have been limited to two seals in this study because stress of a new captive environment may have limited breeding behaviour in new seals.

Haul outs occurred regularly throughout the year and seals spent approximately 14 % of each day hauled out. Percentage of the day spent hauled out (pooled data) did not significantly vary from season to season. Also, individual results showed that only three of nine seals varied significantly across seasons. These results suggest, as do preliminary data from field studies (G. Stenson and T. Haug, pers. comm.), that harp seal haul out is not limited to the lactation and moult periods as once assumed (Sergeant 1965; 1991; Ronald and Dougan 1982). Free-ranging harp seals may haul out on a regular basis (when substrates are available) to sleep because a hauled out seal does not have to expend energy contending with waves and currents. In this study, the continuous inflow of sea water to the tanks created a strong circular current. Floating seals were observed "bumping" into the tank wall when sleeping. Therefore, it probably was less disturbing for seals to haul out for rest. Seals may also haul out during the entire year for routine skin growth and maintenance (Feltz and Fay 1966). However, it appears that haul out is not required for rest and skin maintenance every day, as seals in this study did not haul out at all on approximately sixty per cent of the study days. Similarly, free-ranging harbour seals spent approximately fifty per cent of the study days at sea and did not haul out during these days (Pitcher and McAllister 1981; Sullivan 1982; Godsell 1988).

Patterns of daily activity were similar throughout the year for each seal and across seals: activity consistently peaked around midday and was lowest at night and in the early morning hours at all seasons, breeding, and moult. Similarly, most seals showed concordance in haul out patterns across seasons. Most haul out occurred late at night and early in the morning, and little around midday. All seals had circadian rhythms of activity. The midday feeding time during the study probably acted as an entraining mechanism for the rhythms as animals began to anticipate food (Bolles and deLorge 1962; Edmonds and Adler 1977). The shift in acrophase (time of peak activity) to approximately an hour earlier in summer than winter further suggests entrainment. During the summer the seals were fed approximately an hour earlier because of the shift in time due to Daylight Savings (time of day advanced 1 h on 7 April 1996). This possible entrainment of captive harp seal activity to a human-determined feeding schedule, suggests that factors like habits of prey (i.e., availability or ease of access to food) may play a role in determining the daily activity patterns of harp seals in the wild (Boulos and Terman 1980). Murie and Lavigne (1991) suggested that the winter feeding on capelin by harp seals in the Gulf of St. Lawrence probably occurred between midnight and the early morning hours. This was the time of day when capelin were evenly dispersed near the surface at 0-20 m and supposedly the easiest time for harp seals to forage on this species. Seasonal changes in daily patterns of activity are likely in the wild, as harp seals are known to have seasonal and geographical variations in their diet throughout their range (Lawson et al. 1995; Wallace and Lawson 1997). Another possible explanation for the shift in acrophase may be due to the changing time of sunrise between winter and summer. Further experimentation (i.e., manipulating the feeding schedule) is needed to provide conclusive evidence of entrainment.

Daily food intake did not directly influence harp seal activity in this study. However, results of the imposed fasting experiment indicate that fasting may decrease activity. Animals are believed to lower activity levels during periods of low food availability due to lowered body condition set-points (Mrosovsky and Sherry 1980; Sherry 1981). The reduction of activity and food intake, despite unrestricted access to food, has been noted in captive harbour seals during moult (Rosen 1995). Similar results may not have been found in this study because for most of the moult period activity data could not be collected. In the wild, activity may decrease during moult when thermoregulatory concerns restrict foraging time. It should be noted that the fasting experiment in this study was based on only two seals, and further investigation is needed to provide conclusive results.

Females spent significantly more time hauled out throughout the year than males. This may be expected in the wild where females haul out to nurse and males do not (Kovacs 1987). However, in this study it is difficult to comment on sexual differences because of the small sample size. In all likelihood, the difference is probably an individualistic one—Rhonda, a female, was the seal with the highest level of haul out, therefore she probably skewed the results for females. New seals were found to be more active than resident seals. This may be attributed to the higher levels of stress this group appeared to be under. All new seals exhibited stereotypic behaviour and resident seals generally did not. Also, all resident seals started moult before any of the seals from the new group did. Resident seals moulted mainly during the time of the year moult occurs in the wild (April and May), while new seals generally did not complete moult until June. This suggests that recent captivity may physiologically affect seals.

Individuality and time of day had the greatest influence on activity and haul out of seals in this study. However, seasonal trends in these behaviours were observed during moult and breeding. Researchers that use bioenergetic models to estimate prey consumption of pinnipeds should incorporate these daily and seasonal variations in activity into their models. Failing to recognize variation in activity can lead to serious errors in prey consumption estimates. This is of particular importance in Newfoundland where the recent decline of cod stocks (Hutchings and Myers 1994; Myers and Cadigan 1995; Myers et al. 1996) has led to questions about the impact of the harp seal on the fishery. Future research in this field should be directed at monitoring activity in free-ranging harp seals where the energetic costs of migration and foraging can be assessed. It is also important to investigate the influence of proximate factors like weather and disturbance on activity and haul out, as discussed in the next chapter.

Chapter 4: The Influence of Weather on Captive Harp Seal Activity and Haul Out

Introduction

Most studies on the effects of weather on pinniped behaviour have focused on species that haul out on land throughout the entire year. It has been suggested that pinnipeds haul out on a regular basis to: sleep (Schneider et al. 1980), avoid predators (Terhune 1985), and maintain skin cells (Feltz and Fay 1966). Much of this research has been conducted in areas where the availability of haul out sites is tide-related and, in most cases, the predominant factor influencing haul out is the tidal cycle (Scheffer and Slipp 1944; Schneider and Payne 1983; Pauli and Terhune 1987; Thompson et al. 1989). Weather conditions explain little or none of the observed variation in phocid numbers in most studies of terrestrial haul out (Salter 1979; Schneider and Payne 1983; Kreiber and Barette 1984; Pauli and Terhune 1987).

Weather appears to have a greater influence on haul out that occurs on ice. For instance, the number of Weddell seals hauled out increased with temperature and solar radiation, and was negatively correlated with wind velocity (Smith 1965; Ray and Smith 1968; Thomas and DeMaster 1983; Wartzok 1991). Similarly, walrus (*Odobenus rosmarus*) generally sought exposure to sunshine and avoided exposure to high winds and precipitation (Fay and Ray 1968). Ringed seals also avoided exposure to high winds (Finley 1979; Smith and Hammill 1981). Stewart (1987) examined the effect of weather on the behaviour of harp seal mother and pups on ice. Of the weather variables investigated, hours of sunlight had the greatest effect (positive) on the amount of time mothers spent hauled out with their pups. Wind velocity and temperature had little effect. Females also spent less time on the ice during overcast or rainy days. Other studies on harp seals, conducted during nursing, have also found peak numbers of animals hauled out during maximal solar radiation (Kovacs 1987; Lydersen and Kovacs 1993).

Harp seals, like other pinnipeds, also haul out during moult (Sergeant 1973). Weather during this time may be of particular importance to pinnipeds because it influences the rate of new hair growth (Feltz and Fay 1966; Fay 1982). Exposure to solar radiation increases skin temperature and accelerates the moult process (Feltz and Fay 1966; Øritsland 1974; Fay 1982) and is used to synthesize vitamin D that is required for hair growth (McLaren 1958). High winds and rainfall have a negative influence on haul out in several species (Fay and Ray 1968; Finley 1979; Smith and Hammill 1981; Stewart 1987). Heat loss through the body surface increases under these conditions (Ohata and Whittow 1974; Øritsland 1974). Therefore, pinnipeds may choose to return to the water to forage (despite heat loss incurred in that medium, Scholander et al. 1950) and to haul out when conditions are more favorable.

Investigation of the influence of weather on haul out of harp seals has been limited to studies conducted during the nursing period (Kovacs 1987; Stewart 1987; Lydersen and Kovacs 1993). Contrary to previous reports (Sergeant 1973; Ronald and Dougan 1982), harp seal haul out occurs outside the breeding and moulting periods (G. Stenson, unpubl. data; T. Haug, pers. comm.). Seasonal variations and shifts in daily haul out pattern have been noted in other pinnipeds (Cameron 1970; Thompson et al. 1989; Kelly and Quakenbush 1990). Therefore, this study included data for an entire year (with continuous 24-h periods) on haul out, and with measures of four weather variables: solar radiation, air temperature, wind velocity, and relative humidity. I predicted that solar radiation and air temperature would have a positive effect on haul out, and that wind velocity and relative humidity would have a negative effect. These effects were expected to be most important during the spring moult. The influence of weather on total activity (both in and out of the water) and aquatic activity (excluding haul out) were also investigated. Although pinnipeds can sleep in water (Ridgway et al. 1975), increases in the amount of time spent hauled out generally led to decreases in overall activity for harbour seals (Rosen 1995). Therefore, I expected that if weather influenced haul out it would indirectly influence activity.

Disturbance generally has a negative influence on haul out (Schneider and Payne 1983; Allen et al. 1984; Davis and Renouf 1987; Pauli and Terhune 1987; Kovacs et al. 1990). Seals generally return to the water when disturbed. Kovacs and Innes (1990) assessed the impact of tourism on harp seals in the Gulf of St. Lawrence and found that females that were disturbed decreased both attendance and nursing duration significantly. Disturbances caused by maintenance activities (such as feeding and cleaning) occurred on a regular basis in the present study. I predicted a negative relationship between harp seal haul out and disturbance.

Method

Collection of Weather Data

Two weather data sets were used to allow analysis of all activity and haul out data. The first set (OSC data) was acquired from a weather station located in the seal compound. Air temperature (°C), global solar radiation ($MJ \cdot m^{-2}$), wind velocity ($km \cdot h^{-1}$), and relative humidity (%) were measured every min and averaged over 30 min from 17 April 1996 to 21 October 1996. A second data set (airport data), containing daily averages of the same weather variables, was acquired from the Environment Canada weather station at the St. John's Airport (5 km west of the seal compound) and included data from 1 September 1995 to 30 September 1996. Pearson's correlation coefficients were calculated to compare these data sets. Airport data were highly correlated with the OSC weather data and therefore were suitable for use.

Data Analysis

Databases with different levels of resolution were used to analyze the influence of weather on total activity, aquatic activity, and haul out. The OSC database was composed of TK-HH, TKW-HH, MOVE, TOWATER, and ONDECK-HH (see Table 2). Additionally, the database contained the 30-min mean values of the weather variables collected at OSC. The airport database contained TK-D, ONDECK-D, the photoperiod of each day, and the daily averages of the weather variables collected at the St. John's airport.

Several approaches were used to assess possible seasonal, daily, and disturbance effects on activity and haul out. Chi-square analyses were conducted to determine if the presence/absence of disturbance and day/night had a significant influence on seal haul out (MOVE, TOWATER, and ONDECK-HH). Consequently, the OSC data were subsampled for haul out analysis, using diurnal-undisturbed data. Data were analyzed according to season to control for possible effects of photoperiod.

Logistic regression was used to analyze haul out in this data set. The response variables were MOVE and TOWATER, and wind velocity, solar radiation, relative humidity (arcsine-transformed), and temperature were the explanatory variables. A similar procedure was used to analyze activity of the seals. The OSC data were subsampled to include only diurnal-undisturbed data. Autoregression (lag n=1) was used to analyze the data with TK-HH and TKW-HH as response variables. This procedure corrected for strong first order autocorrelation introduced by the sequential sampling of activity and weather variables.

The same approach was taken with the airport data. Once again, the data were divided into seasons to control for possible effects of photoperiod on activity and haul out. Solar radiation was divided by photoperiod to control for possible photoperiod effects within season. TK-D and ONDECK-D (arcsine-transformed) were used as response variables in an autoregression (lag n=1) procedure with solar radiation, wind velocity, relative humidity (arcsine transformed), and temperature as explanatory variables. All analyses were done for individual seals for each season.

Results

Highest mean temperature (14.1 °C) and solar radiation level (0.7 MJ · m^{-2}) occurred in summer, and slightly lower relative humidity and wind velocity occurred then (Table 22). The lowest temperature (-14.2 °C) and highest wind velocity (57.0 km · h^{-1}) occurred in winter; fall and spring were intermediate (Table 22).

Both disturbance and occurrence of day or night had significant effects on seal haul out (Table 23). MOVE and TOWATER were greater when seals were disturbed. Most (six of nine) seals had higher levels of ONDECK-HH when there was no disturbance and at night.

Wind velocity had a significantly negative effect on ONDECK-D for six of nine seals (Table 24). Conversely, wind velocity had a significantly positive influence on both TK-HH and TK-D (Tables 25, 26). This was more prevalent during the spring season.

Solar radiation was positively associated with ONDECK-D for four seals, most notably during the spring (Table 25). Table 26 shows that TK-HH was positively correlated with solar radiation for six seals, mainly during the summer. However, TKW-HH (Table 27) showed the opposite response in spring.

Relative humidity had a significantly positive influence on TK-HH (Tables 26) and TK-D (Table 25), and had a negative influence on ONDECK-D (Table 24). However, this was only observed for a few seals. Relative humidity significantly influenced TKW-HH for more seals (Table 27). This occurred mainly in spring.

Temperature had a significantly negative effect on TK-HH for four seals during different seasons (Table 26). ONDECK-D was negatively correlated with temperature in

Table 22. Summary of airport weather data.

Weather variable	Fall			Winter			Spring			Summer		
	Mean ± s.d.	Min.	Max.	Mean ± s.d.	Min.	Max.	Mean ± s.d.	Min.	Max.	Mean ± s.d.	Min.	Max.
Solar radiation ($MJ \cdot m^{-2}$)	0.2 ± 0.17	0.0	0.7	0.3 ± 0.17	0.0	0.8	0.6 ± 0.32	0.0	1.2	0.7 ± 0.29	0.0	1.3
Temperature (°C)	4.7 ± 5.44	-9.0	15.8	-2.9 ± 4.92	-14.3	11.3	4.4 ± 4.71	-6.7	16.7	14.1 ± 3.81	5.8	23.5
Wind velocity ($km \cdot h^{-1}$)	23.5 ± 9.20	5.0	55.3	25.7 ± 11.71	7.0	57.0	21.1 ± 7.38	6.8	39.1	20.3 ± 7.61	6.7	40.1
Relative humidity (%)	86.4 ± 8.42	63.7	100.0	85.3 ± 10.42	55.0	100.0	84.6 ± 10.91	57.3	99.3	82.5 ± 7.65	61.4	97.0

Note: Min. = minimal value, Max. = maximal value.

Table 23. Disturbance and day/night significantly influenced the haul out of most seals. Comments indicate significant Chi-square results; other results were not significant.

	Disturbance			Day/night		
Seal	MOVE	TOWATER	ONDECK-HH	MOVE	TOWATER	ONDECK-HH
Ba	> when dist.	> when dist.		> at day		
Ch			< when dist.	> at day		
El			< when dist.			> at night
Ja	> when dist.	> when dist.	< when dist.		> at night	> at night
Mc	> when dist.	> when dist.				> at night
Rh			< when dist.	> at night	> at night	> at night
Ty	> when dist.	> when dist.	< when dist.	> at day		
Vc	< when dist.					> at night
Vg	> when dist.	> when dist.	< when dist.		> at night	> at night

Note: "when dist." = when disturbed.

Table 24. Relationships of ONDECK-D to weather variables based on autoregression analysis (+ = significant positive, - = significant negative results; other results were not significant).

Seal	Temperature	Solar radiation	Relative humidity	Wind velocity
Ba			-fall	- fall
Ch	- summer		- fall - spring	- spring -summer
El[a]				- winter
Ja[b]				
Mc	+ spring	+ fall		- spring
Rh[c]	- summer			
Ty		+ spring		- spring
Vc		+ spring	- fall	
Vg	+ spring - summer	+ spring		- fall - spring

[a] El data only for winter
[b] Ja data only for spring and summer
[c] Rh data only for summer and winter

Table 25. Relationships of TK-D to weather variables based on autoregression analysis (+ = significant positive, - = significant negative results, other results were not significant).

Seal	Temperature	Solar radiation	Relative humidity	Wind velocity
Ba				+ fall
Ch			+ winter	+ fall
El[a]				
Ja[b]				+ spring
Mc		- spring		+ spring
Rh[c]			+ winter	
Ty		- spring	- spring + summer	+ spring
Vc		- spring	+ fall	
Vg		- spring		+ spring + fall

[a] El data only for winter
[b] Ja data only for spring and summer
[c] Rh data only for summer and winter

Table 26. Relationships of TK-HH to weather variables based on autoregression analysis (+ = significant positive, - = significant negative; other results were not significant).

Seal	Temperature	Solar radiation	Relative humidity	Wind velocity
Ba			+ spring + fall	+ spring + fall
Ch		+ fall		+ fall
El	- spring - fall	+ summer + fall	+ summer	
Ja[a]	- spring			
Mc[b]		+ summer		+ spring
Rh	- fall - summer	+ summer		+ summer
Ty		+ summer		+ spring
Vc				+ summer
Vg	- spring -summer	+ summer	+ fall	+ spring + fall

[a] Ja data only for spring and summer
[b] Mc data only for spring and summer

Table 27. Relationships of TKW-HH to weather variables based on autoregression analysis (+ = significant positive, - = significant negative results; other results were not significant).

Seal	Temperature	Solar radiation	Relative humidity	Wind velocity
Ba		- spring + summer + fall	+ spring + fall	+ spring
Ch		+ fall	+ spring + summer	
El		+ summer + fall	+ spring	
Ja[a]		- spring		
Mc[b]	-summer	- spring + summer		
Rh	- summer	+ summer		+ summer
Ty		- spring + summer	+ spring + summer	
Vc		- spring		
Vg	-summer	+ summer + fall	+ fall	

[a] Ja data only for spring and summer
[b] Mc data only for spring and summer

summer and positively correlated in spring for four seals (Table 24). Temperature was negatively associated with TKW-HH during the summer but only for three seals (Table 27).

Temperature, solar radiation, relative humidity, and wind velocity did not significantly influence TOWATER (Table 28). An increase in solar radiation significantly increased the probability of MOVE in four seals during spring and fall. Wind velocity also significantly increased the likelihood of MOVE in three seals, while relative humidity had the opposite effect in four seals. Increased temperature decreased the odds of MOVE in five seals during spring and summer.

Table 28. Effects of weather variables on MOVE and TOWATER (excluding disturbance and nighttime) based on logistic regression analysis. Odds-Ratio values are given in brackets for significant results; other results were not significant.

Seal	Temperature		Solar radiation		Relative humidity		Wind velocity	
	MOVE	TOWATER	MOVE	TOWATER	MOVE	TOWATER	MOVE	TOWATER
Ba	spring (0.72)		fall (1.19) spring (1.11)					
Ch								
El	summer (0.78)				summer (0.84)			
Ja[a]	summer (1.12)		spring (1.08)		spring (0.72) summer (0.89)			
Mc[b]	spring (0.82)							
Rh	summer (0.91)		spring (1.05)		summer (0.87)		summer (1.05)	
Ty			spring (1.07)		spring (0.79)		spring (1.11)	
Vc								
Vg							summer (1.10)	

[a] Ja data only for spring and summer

[b] Mc data only for spring and summer

Discussion

Both weather and disturbance affected activity and haul out of captive harp seals in this study. Human disturbance was significantly associated with seals returning to the water and the seals tended to spend more time hauled out when they were undisturbed. This is consistent with findings from other pinniped studies (Schneider and Payne 1983; Allen et al. 1984; Davis and Renouf 1987; Pauli and Terhune 1987; Kovacs and Innes 1990). Although disturbance influenced haul out patterns, it did not prevent seals from hauling out on a regular basis. Similarly, Kovacs and Innes (1990) found that while tourist disturbance decreased both attendance and nursing in mother and pup harp seals, behaviour patterns returned to normal shortly after disturbances stopped. Most seals in this study tended to haul out more frequently at night, as did captive walrus (Fay and Ray 1968).

During the day, and in the absence of disturbance, the level of solar radiation influenced the haul out and activity of most seals. It was positively associated with mean per cent of the day spent hauled out and negatively associated with mean daily activity. It was also positively associated with MOVE in four seals. These results occurred primarily during spring when most seals underwent moult. Seals may show an increased tendency to haul out on sunny days because radiation is used to synthesize vitamin D that is utilized during hair growth (McLaren 1958), and heating of the skin accelerates the moult process (Feltz and Fay 1966; Fay 1982). When examined on a finer scale (half hour), solar radiation had a significantly positive effect on total activity in the summer for five of nine seals. This relationship may be a result of events related to time of day rather than solar radiation. Although feeding time was excluded from all analyses, the time preceding feeding was not. Seals anticipated feeding and increased activity around the time (midday) when solar radiation levels also happen to be high. However, during the spring TKW-HH was negatively correlated with solar radiation. This seems to contradict the previous argument. Kooyman (1975) suggested that Weddell seals use vision as an important sensory modality and this was partially supported by findings of correlation of depth-time profile characteristics with light levels: night or twilight dives were all shallower compared to dives during daylight conditions. The harp seals in this study may have shown similar increased levels of aquatic activity with increasing solar radiation because light better penetrated the tank waters during these times.

Surprisingly, air temperature did not affect the haul out of most animals during the spring. I expected that a greater effect would be observed during the spring moult because heating of the skin accelerates the growth of skin and hair, and hence is energetically beneficial to the animal (Feltz and Fay 1966; Fay 1982). The apparent lesser importance of air temperature compared to solar radiation is consistent with other harp seal studies (Stewart 1987; Lydersen and Kovacs 1993). However, these studies were performed during lactation, not moult. During the summer, air temperature had a negative influence on ONDECK-D. Seals may avoid or reduce haul out on warmer days to prevent potential hyperthermia. Watts (1992) found similar seasonal effects in harbour seals. Total number of seals hauled out decreased during the summer as seals theoretically gained net heat from their environment. During spring, when heat levels and the risk of hyperthermia were lower, maximum daily haul out numbers of seals were recorded.

Increased wind velocity was associated with decreased per cent of the day spent hauled out for six seals. Weddell seals (Smith 1965; Ray and Smith 1968; Thomas and DeMaster 1983; Wartzok 1991), walrus (Fay and Ray 1968), and ringed seals (Finley 1979; Smith and Hammill 1981) show the same behavioural response, but nursing harp seal mothers seemed unaffected by wind velocity (Stewart 1987). Seals in this study generally did not haul out when winds were high during spring. This is probably a reflection of seals avoiding conditions that did not favour epidermal mitosis and growth of new hair (Feltz and Fay 1967; Øritsland 1974). Higher wind velocity was also associated with increases in TK-D and TK-HH in fall, spring, and summer for several animals. This increase in total activity may be a result of the decrease in haul out (and lower activity) associated with high winds. Another possible explanation is that the roughened water surface in the tanks created by high winds, may have disrupted normal surface swimming of the seals, and increased activity as the seals were required to swim more vigorously to elevate their noses clear of the disturbed water surface to breath. The first explanation is probably more plausible since wind velocity significantly influenced the behaviour of only two seals when haul out behaviour was excluded from activity data.

Relative humidity influenced the aquatic activity of more seals than it did their haul out. The haul out of three seals was negatively influenced by relative humidity. Contrary to initial predictions, this effect was observed during the fall and not during spring. Although fall had the highest relative humidity, this is an unlikely reason for decreased haul out compared to other seasons, since seals in these seasons also had increased levels of aquatic activity associated with higher relative humidity levels. On humid days, some seals (four) decreased the amount of movement to the deck, or to the water in spring and summer. Increases in relative humidity deterred seals from haul out and consequently may have resulted in increases in overall activity values.

This study demonstrates the importance of investigating the relationship between weather and seal behaviour on a fine temporal scale, and during all seasons. Summaries of data for entire days suggested there were few seals influenced by weather, whereas data examined at half-hourly scales indicated greater response to these meteorological variables. In an extreme instance, temperature had no effect on daily activity, yet it showed substantive effect at the half-hour level.

The winter of 1995-1996 was abnormally mild and there were no extremely cold temperatures (often associated with reduced haul out; Fay and Ray 1968; Boulva and McLaren 1979). This may explain why weather had relatively little influence upon activity and haul out during winter. Weather also exhibited inconsistent influence upon activity and haul out depending on season; solar radiation positively affected activity in the summer but had the opposite effect in spring. Seasonal variation in behavioural response to weather has been noted in other pinnipeds, for both captive (Fay and Ray 1968) and free-ranging animals (Smith and Hammill 1981; Watts 1992; Trites and Antonelis 1994; Grellier et al. 1996), but never for harp seals before now.

There was a high degree of individual behavioural variation in this study. All seals never showed the same response to weather conditions in the same season. Individual variation in seal behaviour has been noted before (Kelly 1979; Ashwell-Erickson et al. 1986; Thompson et al. 1989). It can be as variable as certain harbour seals in a group preferring to haul out at night and others in the day (Yochem et al. 1987; Thompson et al. 1989). Therefore, it is not surprising that captive individuals in this study were variable in their response to weather.

Although captive studies cannot emulate wild conditions resulting in migration and foraging behaviour, they do permit baseline data collection on a fine scale for extended periods of time. Previous harp seals studies that have investigated weather influences have been restricted to the lactation period (Kovacs 1987; Stewart 1987; Lydersen and Kovacs 1993). Although these studies detected positive influences of solar radiation on haul out they could not investigate possible seasonal variation in this response. This study demonstrated the effect of solar radiation and wind velocity, and to a lesser extent air temperature and relative humidity, on haul out and activity (especially during moult), and how reversal of trends can occur among seasons. These findings may be important to researchers conducting aerial survey counts of harp seals. More accurate survey counts may be obtained during moult, and under clear (increased solar radiation), calm (low wind velocity), and undisturbed conditions, when seals generally increase their time spent hauled out.

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Appendix A: Feeding Schedule

Table A-1. Feeding schedule of seals during the study period. Atlantic herring was fed at times not listed.

Prey type	Begin date	End date	Seals
Arctic cod	27-Jan-96	06-Feb-96	Ba, Mc, Rh
	28-Jan-96	06-Feb-96	Ty
Atlantic cod	22-Sep-95	10-Oct-95	Ch, Mc,
	15-Mar-96	25-Mar-96	Ba, Mc, Ty
	17-Mar-96	25-Mar-96	Rh
Atlantic herring + American plaice	06-Jul-96	09-Jul-96	Vc
	11-Jul-96	11-Jul-96	Ba, Vc
Atlantic herring + Arctic cod	15-Jul-96	15-Jul-96	Ba, Ty, Vc
	27-Jan-96	27-Jan-96	Ty
Atlantic herring + squid	02-Apr-96	02-Apr-96	Vc
	10-May-96	10-May-96	Ty
	23-Jun-96	23-Jun-96	Ba
Capelin	21-Oct-95	09-Nov-95	Ba, Ch, El, Mc, Vc, Vg
Greenland halibut	13-Feb-96	23-Feb-96	Ba, Mc, Ty
Redfish	16-Apr-96	16-Apr-96	Rh
	16-Apr-96	18-Apr-96	Ba, Mc
	27-May-96	30-May-96	Vc
	27-May-96	31-May-96	Ch
	27-May-96	04-Jun-96	Ty
Sand lance	07-Jun-96	18-Jun-96	Ba, Rh, Ty, Vc
Squid	24-Jun-96	05-Jul-96	Ba, Vc
	10-Jul-96	10-Jul-96	Ba, Vc
Fast	11-Sep-95	21-Sep-95	Ba, Ch, Mc
	11-Sep-95	02-Oct-95	El
	11-Oct-95	20-Oct-95	Ba, Ch, El, Mc, Vc
	25-Jan-96	26-Jan-96	Ba, Ch, El, Mc, Rh, Ty, Vc, Vg

Table A-1.
(continued)

13-Feb-96	15-Feb-96	Rh
15-Mar-96	16-Mar-96	Rh
16-Apr-96	18-Apr-96	Ty
17-Apr-96	18-Apr-96	Rh
18-Apr-96	18-Apr-96	Vc
25-May-96	26-May-96	Ba, Ch, El, Mc, Rh, Vc, Vg
22-Jun-96	22-Jun-96	Ba, Ch, El, Ja, Mc, Rh, Ty, Vc, Vg
14-Jul-96	14-Jul-96	Ba, Ch, El, Ja, Mc, Rh, Ty, Vg
11-Aug-96	12-Aug-96	Ba, Ch, El, Ja, Mc, Rh, Vg
28-Sep-96	28-Sep-96	Ba, Ch, El, Ja, Mc, Rh, Vg
05-Oct-96	05-Oct-96	Ba, Ch, El, Ja, Mc, Rh, Vg

Appendix B: Deployment Schedule

Table B-1. AR deployment dates for each seal during the study period.

	Deployment Periods			
Seal	No.	Length (days)	Begin date	End date
Ba	1	28	26-Oct-95	22-Nov-95
Ba	2	27	24-Nov-95	20-Dec-95
Ba	3	18	20-Dec-95	06-Jan-96
Ba	4	7	11-Feb-96	17-Feb-96
Ba	5	10	27-Feb-96	07-Mar-96
Ba	6	14	19-Mar-96	01-Apr-96
Ba	7	3	04-Apr-96	06-Apr-96
Ba	8	32	30-Apr-96	31-May-96
Ba	9	24	01-Jun-96	24-Jun-96
Ba	10	38	24-Jun-96	31-Jul-96
Ba	11	4	01-Aug-96	04-Aug-96
Ba	12	11	11-Aug-96	21-Aug-96
Ba	13	56	26-Aug-96	19-Oct-96
Total	13	272		
Ch	1	9	20-Sep-95	28-Sep-95
Ch	2	26	28-Sep-95	23-Oct-95
Ch	3	14	10-Nov-95	23-Nov-95
Ch	4	32	13-Dec-95	12-Jan-96
Ch	5	12	12-Jan-96	23-Jan-96
Ch	6	39	17-Feb-96	25-Mar-96
Ch	7	21	28-Mar-96	16-Apr-96
Ch	8	20	16-Apr-96	04-May-96
Ch	9	52	10-Jun-96	31-Jul-96
Ch	10	69	13-Aug-96	19-Oct-96
Total	10	294		
El	1	12	20-Sep-95	01-Oct-95
El	2	34	20-Dec-95	22-Jan-96
El	3	38	22-Jan-96	28-Feb-96
El	4	8	18-Apr-96	25-Apr-96
El	5	12	26-Apr-96	07-May-96
El	6	20	23-Jul-96	11-Aug-96
El	7	18	20-Sep-96	06-Oct-96
Total	7	142		

Table B-1.
(continued)

Ja	2	39	18-Apr-96	26-May-96
Ja	3	51	01-Jun-96	31-Jul-96
Ja	4	10	06-Aug-96	15-Aug-96
Total	3	100		
Mc	1	8	13-Sep-95	20-Sep-95
Mc	2	36	20-Sep-95	25-Oct-95
Mc	3	28	10-Nov-95	07-Dec-95
Mc	4	28	07-Dec-95	03-Jan-96
Mc	5	26	04-Jan-96	29-Jan-96
Mc	6	21	31-Jan-96	20-Feb-96
Mc	7	17	20-Mar-96	05-Apr-96
Mc	8	10	22-May-96	31-May-96
Mc	9	23	01-Jun-96	23-Jul-96
Mc	10	11	12-Sep-96	22-Sep-96
Total	10	208		
Rh	1	7	15-Dec-95	21-Dec-95
Rh	2	37	04-Jan-96	09-Feb-96
Rh	3	21	09-Feb-96	29-Feb-96
Rh	4	14	15-Mar-96	28-Mar-96
Rh	6	4	24-Apr-96	27-Apr-96
Rh	7	32	11-Jun-96	12-Jul-96
Rh	8	20	12-Jul-96	31-Jul-96
Rh	9	26	26-Sep-96	21-Oct-96
Total	8	163		
Ty	1	5	10-Nov-95	14-Nov-95
Ty	2	29	17-Nov-95	15-Dec-95
Ty	3	34	15-Dec-95	17-Jan-96
Ty	4	42	17-Jan-96	27-Feb-96
Ty	5	12	14-Mar-96	25-Mar-96
Ty	7	9	23-May-96	31-May-96
Ty	8	43	01-Jun-96	12-Jul-96
Ty	9	20	12-Jul-96	31-Jul-96
Total	8	194		
Vc	1	23	19-Oct-95	10-Nov-95
Vc	2	12	29-Nov-95	09-Dec-95

Table B-1.
(continued)

Vc	4	15	14-Feb-96	28-Feb-96
Vc	5	21	14-Mar-96	03-Apr-96
Vc	6	12	15-May-96	26-May-96
Vc	7	5	27-May-96	31-May-96
Vc	8	51	01-Jun-96	21-Jul-96
Total	7	139		
Vg	1	27	27-Oct-95	22-Nov-95
Vg	2	26	25-Nov-95	20-Dec-95
Vg	3	34	20-Dec-95	22-Jan-96
Vg	4	38	22-Jan-96	28-Feb-96
Vg	5	25	18-Mar-96	11-Apr-96
Vg	6	12	15-May-96	26-May-96
Vg	7	50	03-Jun-96	22-Jul-96
Vg	8	17	20-Sep-96	06-Oct-96
Total	8	229		
Grand Total	74	1741		

Appendix C: Ethogram

Table C-1. Ethogram for captive harp seals.

Category	Symbol	Description
Below surface	BE	Subject's entire body is beneath the water surface.
180° roll	18	Subject turns 180° from dorsal to ventral, or ventral to dorsal, or left lateral to right lateral, or right lateral to left lateral.
360° roll	36	Subject turns 360° from dorsal to dorsal, or ventral to ventral, or left lateral to left lateral, or right lateral to right lateral.
Upright	UP	Subject is stationary (no movement through water) with only head and neck above water surface in vertical position.
Inverse upright	IU	Subject is stationary (no movement through water) with only rear flippers above water surface in vertical position.
Social interaction	SI	Subject deliberately approaches or touches another subject.
Haul out	HO	Subject's entire body is out of the water and on the ramp, ramp platform, or deck.
Vocalization	VO	Subject vocalizes while hauled out.
Vocalization	VC	Subject vocalizes while at the water's surface.
Play	PL	Subject "plays" with object that has no apparent benefit (i.e. drain pipe, drain pipe cover).
Forward roll	FR	Subject goes below surface headfirst while swimming ventrally, and rest of body follows.
Backwards roll	DR	Subject goes below surface headfirst while swimming dorsally, and rest of body follows.

Table C-1. (continued)

Lateral roll	LR	Subject goes below surface headfirst while swimming laterally, and rest of body follows.
Front porpoise	FP	Subject surfaces quickly (head first) and the ventrum faces the water and the dorsum faces the sky. The body has space between itself and the water before the subject reenters the water, ventrum first.
Back porpoise	DP	Subject surfaces quickly (head first) and the dorsum faces the water and the ventrum faces the sky. The body has space between itself and the water before the subject reenters the water, dorsum first.
Lateral porpoise	LP	Subject surfaces quickly (head first) and one lateral surface faces the water and the other faces the sky. The body has space between itself and the water before the subject reenters the water laterally.
Ventral float	VF	Subject moving inactively at water surface, floating with ventrum in the water and dorsum out of the water.
Dorsal float	DF	Subject moving inactively at water surface, floating with dorsum in the water and ventrum out of the water.
Lateral float	LF	Subject moving inactively at water surface, floating with one side in the water and one side out of the water.
Slow ventral swim	SV	Subject swims at the surface with its ventrum in the water, no splash is generated by this action.
Medium ventral swim	MV	Subject swims at the surface with its ventrum in the water, slight splash is generated by this action.
Fast ventral swim	FV	Subject swims at the surface with its ventrum in the water, tremendous splash is created from this porpoise-like action.
Slow dorsal swim	SD	Subject swims at the surface with its dorsum in the water, no splash is generated by this action.
Medium dorsal swim	MD	Subject swims at the surface with its dorsum in the water, slight splash is generated by this action.

Table C-1. (continued)

Fast dorsal swim	FD	Subject swims at the surface with its dorsum in the water, tremendous splash is created this porpoise-like action.
Slow lateral swim	SL	Subject swims at the surface with one side in the water, no splash is generated by this action.
Medium lateral swim	ML	Subject swims at the surface with one side in the water, slight splash is generated by this action.
Fast lateral swim	FL	Subject swims at the surface with one side in the water, tremendous splash is created from this porpoise-like action.

Appendix D: Multiple Regression Fit Program

The program (Klemfuss and Clopton 1993) used a multiple regression fit to an equation of the form:

$$y = (a + b_1)(\cos(2\pi t) + b_2)(\sin(2\pi t))$$

where y is the actual data value (TK-HH), a is the intercept constant estimated by the regression, b_1 is the cosine coefficient estimated by the regression, b_2 is the sine coefficient estimated by the regression, and t is the time for each y, expressed as t divided by the trial tau (in this case 24.1).

Detailed definitions of the statistics produced by the program are listed below and illustrated on the following page.

1. amplitude: a measure of extent of rhythmic change—the difference between the maximum and the mesor of a function used to approximate the rhythm (Halberg and Lee 1974)
2. mesor: rhythm-determined average, midway between the highest and lowest values of function used to approximate a rhythm
3. computative acrophase: the lag from midnight of day 1 to the crest time in the function used to approximate a rhythm

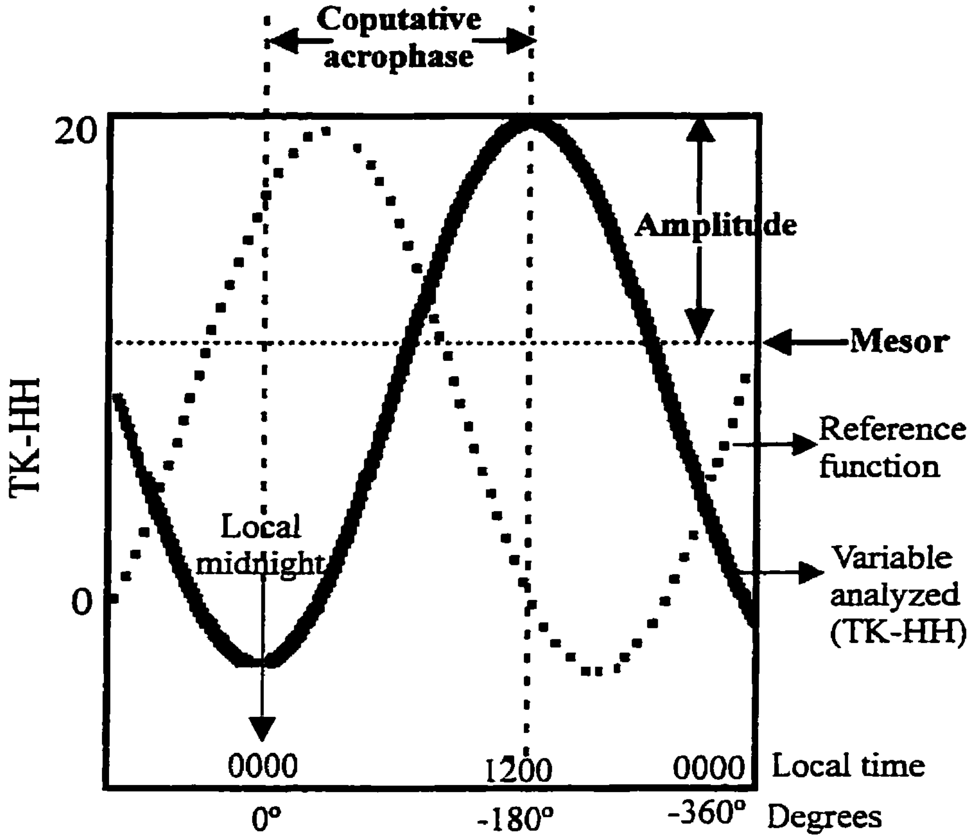

Figure D-1. Rhythm statistics produced by the multiple regression fit program (Klemfuss and Clopton 1993).

Appendix E: Activity Autocorrelation Results

Table E-1. Results of TK-HH autocorrelation for Babette. All lags shown are significant at $\alpha = 0.5$.

Deployment period	Lag	t-ratio	Deployment period	Lag	t-ratio	Deployment period	Lag	t-ratio
26 Oct - 22 Nov 1995	2	-15.76	27 Feb- 7 Mar 1996	2	-8.79	24 Jun- 31 Jul 1996	2	-29.23
	4	-7.58		4	-2.35		8	-3.72
	10	-3.43		21	-3.82		14	-3.22
	16	-3.12		23	-2.66		17	-3.53
	19	-2.88		25	3.58		21	-8.77
	21	-7.83		34	2.39		22	3.13
	23	-3.88		44	3.32		23	-4.92
	24	-2.84					25	5.17
	25	2.31	19 Mar - 1 Apr 1996	2	-32.93		26	-2.62
	26	2.73		20	2.74		27	-2.08
	27	2.02		21	-8.92		29	2.70
	29	2.09		25	4.28		33	2.05
	37	2.59		26	-1.98		42	2.35
	41	2.57		34	2.05		44	3.44
	42	2.21		40	-2.49		48	-4.31
	44	2.81		42	3.43			
	45	-2.52				11 Aug - 21 Aug 1996	2	-6.25
	50	-2.11	30 Apr - 31 May 1996	2	-14.55		6	-3.19
				4	-3.02		17	-2.35
24 Nov- 20 Dec 1995	2	-10.83		16	3.74		18	2.25
	6	-2.51		21	-12.46		21	-4.27
	10	2.23		23	-3.26		23	-4.05
	18	2.24		32	2.54		42	2.70
	21	-7.58		38	2.13			
	23	-10.00		47	2.55	26 Aug- 19 Oct 1996	2	-12.70
	24	2.94		48	-2.99		4	-3.19
	36	2.58					6	-2.48
			1 Jun- 24 Jun 1996	2	-14.24		18	3.31
20 Dec 1995- 6 Jan 1996	2	-16.32		4	-3.83		19	-2.81
	4	-3.06		17	-2.52		21	-11.60
	8	-4.51		21	-7.47		23	-10.09
	11	-2.37		23	-4.36		27	2.28
	21	-4.56		24	3.54		28	2.41
	22	3.44		25	2.40		42	3.66
	23	-3.21		42	3.61		46	2.41
	25	3.21		48	-2.69		48	-4.91
	27	2.13		50	2.45		50	-2.02
	34	2.12						
11 Feb- 17 Feb 1996	2	-9.71						
	18	2.65						
	21	-4.54						
	42	3.02						
	48	-2.30						

Table E-2. Results of TK-HH autocorrelation for Chelsea. All lags shown are significant at $\alpha = 0.5$.

Deployment period	Lag	t-ratio	Deployment period	Lag	t-ratio
20-28 Sep 1995	1	-11.11	28 Mar - 16 Apr 1996	1	-24.48
	5	-2.67		2	1.97
	8	-2.62		3	-2.97
	12	-2.32		28	2.42
	15	2.48			
	21	2.18	16 Apr - 4 May 1996	1	-28.59
	25	2.30		2	2.73
	32	-2.64		4	-2.15
				10	2.67
28 Sep - 23 Oct 1995	1	-44.28		24	2.12
	4	-4.17			
	10	2.73	10 Jun - 31 Jul 1996	1	-48.08
	46	-3.43		2	8.63
	49	2.43		3	-5.55
				4	2.52
10-23 Nov 1995	1	-40.45		9	2.78
	22	-2.05		46	-3.87
	47	-2.08		47	2.11
	48	2.71			
			13 Aug - 19 Oct 1996	1	-56.42
13 Dec1995 - 12 Jan 1996	1	-34.38		4	-2.42
	2	3.15		15	2.28
	3	-2.58		26	2.69
	24	2.24		36	-3.47
	26	-2.54		45	-3.66
	48	-3.16		48	-2.86
	50	2.95			
12-23 Jan 1996	1	-20.40			
	2	2.65			
	5	-3.08			
	24	2.89			
17 Feb - 25 Mar 1996	1	-61.55			
	5	-2.74			
	7	2.13			
	8	-1.97			
	9	2.26			
	20	-3.04			
	21	2.39			
	45	-4.30			
	50	2.25			

Table E-3. Results of TK-HH autocorrelation for Elmo. All lags shown are significant at $\alpha = 0.5$.

Deployment period	Lag	t-ratio	Deployment period	Lag	t-ratio
20 Sep – 1 Oct 1995	1	-25.64	20 Sep – 6 Oct 1996	1	-22.43
	48	-4.18		2	-3.77
				8	-3.59
20 Dec 1995 – 22 Jan 1996	1	-34.53		10	5.89
	2	5.30		14	-3.87
	4	-4.08		15	3.36
	8	-2.34		16	2.26
	12	-2.78		17	-4.48
	17	2.13		19	3.05
	24	3.44		22	-3.77
	31	-2.09		24	4.59
	32	2.13		27	-3.19
	33	-2.49		30	-2.38
	42	-2.76		31	2.84
	44	1.98		41	-3.57
				44	4.33
22 Jan – 28 Feb 1996	1	-43.74		45	-2.71
	4	-3.36		46	2.28
	8	-2.12		47	-3.70
	10	2.04			
	31	-2.50			
18-25 Apr 1996	1	-21.39			
26 Apr – 7 May 1996	1	-20.40			
	2	2.41			
	5	-3.84			
	29	2.33			
23 Jul – 11 Aug 1996	1	-21.94			
	4	-2.95			
	17	2.74			
	24	2.34			
	48	-4.91			

Table E-4. Results of TK-HH autocorrelation for Jamie. All lags shown are significant at $\alpha = 0.5$.

Deployment period	Lag	t-ratio
18 Apr – 26 May 1996	1	-54.45
	7	-2.31
	24	3.31
	33	2.69
	37	-3.23
	44	-2.96
1 Jun – 31 Jul 1996	1	-40.13
	5	-2.78
	25	2.21
	44	-2.04

Table E-5. Results of TK-HH autocorrelation for Mickey. All lags shown are significant at $\alpha = 0.5$.

Deployment period	Lag	t-ratio	Deployment period	Lag	t-ratio
13-20 Sep 1995	1	-12.17	31 Jan - 20 Feb 1996	1	-15.22
	2	-2.02		2	-2.48
	27	2.06		5	-2.23
	48	-2.77		23	2.55
	49	2.02		44	-3.46
				49	-2.90
20 Sep - 25 Oct 1995	1	-36.65			
	5	-5.68	20 Mar – 5 Apr 1996	1	-15.65
	26	4.14		3	-2.03
	40	-2.94		11	-2.89
	44	-3.21		19	2.84
	48	-2.03		37	-2.05
				47	-4.01
10 Nov - 7 Dec 1995	1	-14.65			
	2	-4.20	22-31 May 1996	1	-11.44
	3	-4.50		2	-2.47
	14	2.21		11	-2.29
	23	2.80		18	3.65
	32	2.81		47	-2.53
	41	-3.57			
	45	-3.35	1 Jun – 31 Jul 1996	1	-38.92
				3	-4.89
7 Dec 1995 - 3 Jan 1996	1	-24.67		16	-2.17
	3	-2.18		17	2.96
	6	-2.88		23	3.33
	16	2.29		31	2.47
	21	2.41		35	-3.07
	32	2.18		41	-2.67
	42	-3.18		47	-2.06
	46	-5.63			
			12-22 Sep 1996	1	-7.97
4-29 Jan 1996	1	-20.17		2	-5.08
	3	-5.27		3	-5.00
	9	-2.15		8	-3.55
	12	1.97		9	4.58
	18	2.05		45	-2.92
	44	-3.20			
	46	-2.94			
	48	-2.71			

Table E-6. Results of TK-HH autocorrelation for Rhonda. All lags shown are significant at $\alpha = 0.5$.

Deployment period	Lag	t-ratio
15-21 Dec1995	1	-17.01
	2	3.02
	14	2.02
	17	-2.05
	21	2.23
4 Jan - 9 Feb 1996	1	-38.46
	4	-4.22
	8	-2.43
	15	3.97
	19	-2.46
	20	2.40
	43	-3.70
	49	-2.21
9-29 Feb 1996	1	-26.92
	3	-2.12
	7	2.68
	8	-2.57
	19	3.04
	47	-2.84
15-28 Mar 1996	1	-21.61
	2	3.00
	9	-2.81
	26	-2.28
	27	2.30
	34	2.70
11 Jun – 12 Jul 1996	1	-36.16
	2	5.19
	9	2.05
	10	-3.48
	12	2.43
	21	2.39
	31	3.42
	32	-2.71
	39	-2.25
	44	-2.80
	48	-3.60
	49	2.60
12-31 Jul 1996	1	-8.14
	2	-3.93
	3	-3.49
	6	-4.13
	10	-4.05
	18	2.96
	22	2.43
	34	-2.79
	46	-2.41
26 Sep –21 Oct 1996	1	-34.48
	6	-2.57
	15	3.34
	21	2.51
	22	-2.14
	36	3.04
	38	-2.60
	43	-3.82
	48	-4.09

Table E-7. Results of TK-HH autocorrelation for Tyler. All lags shown are significant at $\alpha = 0.5$.

Deployment period	Lag	t-ratio	Deployment period	Lag	t-ratio
17 Nov – 15 Dec 1995	1	-38.30	14-25 Mar 1996	1	-30.50
	6	-4.10		30	2.79
	7	2.41		39	-2.24
	13	-2.87		43	2.29
	15	2.00		48	-2.91
	27	2.64		50	2.45
	43	-2.23			
	44	2.22	23-31 May 1996	1	-25.17
				23	2.65
15 Dec 1995 - 17 Jan 1996	1	-30.10		27	2.32
	2	4.75		28	-2.18
	3	-2.14			
	5	-2.30	1 Jun - 12 Jul 1996	1	-47.09
	11	2.66		4	-4.19
	23	2.58		11	-2.37
	30	2.99		12	3.53
	41	2.01		13	-2.29
	42	-2.75		17	2.15
	45	-3.51		19	-2.76
	48	-2.10		20	2.15
	50	2.08		42	-3.87
				49	-2.74
17 Jan – 27 Feb 1996	1	-27.33			
	2	-7.71	12 – 31 Jul 1996	1	-27.85
	3	6.23		11	-2.54
	4	-6.26		15	-2.39
	5	3.68		16	2.46
	6	-2.83		22	3.04
	7	3.52		28	2.02
	8	-3.51		36	-2.19
	14	-2.43		41	-2.62
	15	3.53		48	-2.64
	16	-3.93			
	18	3.09			
	23	2.59			
	28	2.74			
	42	-2.19			

Table E-8. Results of TK-HH autocorrelation for Victor. All lags shown are significant at $\alpha = 0.5$.

Deployment period	Lag	t-ratio
29 Nov - 9 Dec 1995	1	-8.58
	2	-3.65
	21	3.80
14-28 Feb 1996	1	-5.58
	14	2.24
	27	2.81
	41	2.13
15-26 May 1996	1	-29.12
	4	-3.25
	14	2.67
	15	-3.54
	36	2.25
	38	-2.16
1 Jun – 21 Jul 1996	1	-28.57
	2	-3.30
	5	-2.52
	9	-2.37
	17	-2.70
	18	2.93
	43	-2.33
	47	-4.01

Table E-9. Results of TK-HH autocorrelation for Virgil. All lags shown are significant at $\alpha = 0.5$.

Deployment period	Lag	t-ratio	Deployment period	Lag	t-ratio
27 Oct – 22 Nov 1995	1	-24.66	18 Mar - 11 Apr 1996	1	-27.60
	2	1.97		2	2.66
	4	-3.83		4	-4.29
	5	2.76		6	3.61
	15	3.45		7	-3.50
	21	2.25		10	2.21
	27	2.07		47	-2.80
	35	2.50			
	45	-2.14	15-26 May 1996	1	-14.02
	46	-2.08		2	-2.20
	48	-3.26		5	-4.35
				27	3.57
25 Nov - 20 Dec 1995	1	-31.32		32	-2.05
	3	2.90			
	4	-3.19	3 Jun - 22 Jul 1996	1	-36.58
	10	2.53		2	2.80
	19	2.54		3	-3.57
	27	3.77		18	3.77
	44	-3.09		46	-3.64
	47	-3.42		48	-3.04
20 Dec 1995 – 22 Jan 1996	1	-34.04	20 Sep – 6 Oct 1996	1	-40.05
	2	5.87		14	-2.19
	3	-2.69		15	2.37
	5	-2.84		19	2.48
	6	2.29		47	-3.79
	11	2.36			
	23	3.44			
	30	3.18			
	41	2.78			
	42	-3.79			
	45	-3.88			
22 Jan - 28 Feb 1996	1	-36.88			
	2	6.38			
	3	-3.89			
	5	2.63			
	20	2.66			
	28	3.07			
	32	-2.45			
	34	2.61			
	35	-2.22			
	46	-3.45			

Appendix F: Activity Periodograms

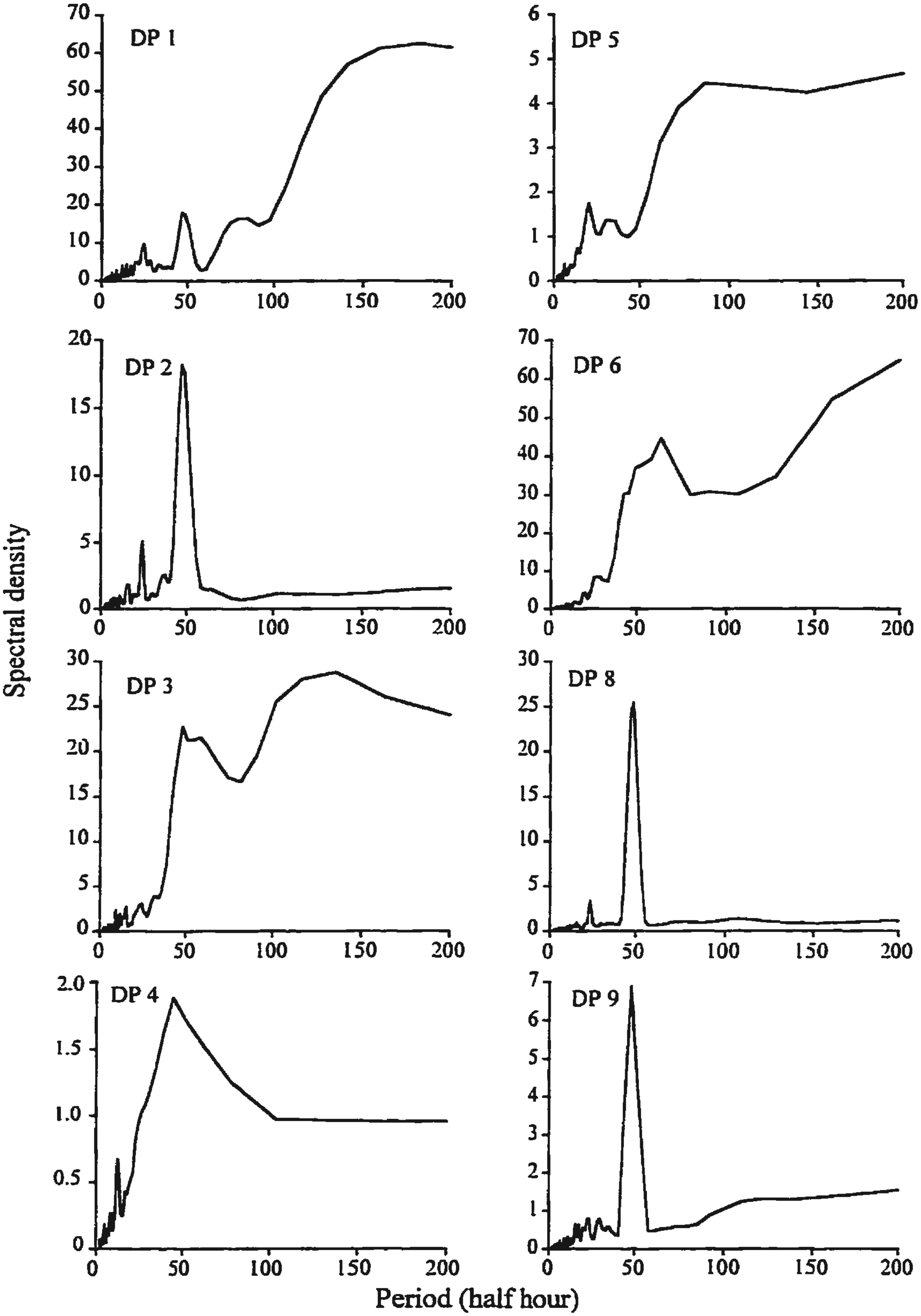

Figure F-1. Activity (TK-HH) periodograms for Babette showing peaks in spectral density generally at period 48 (DP=deployment period).

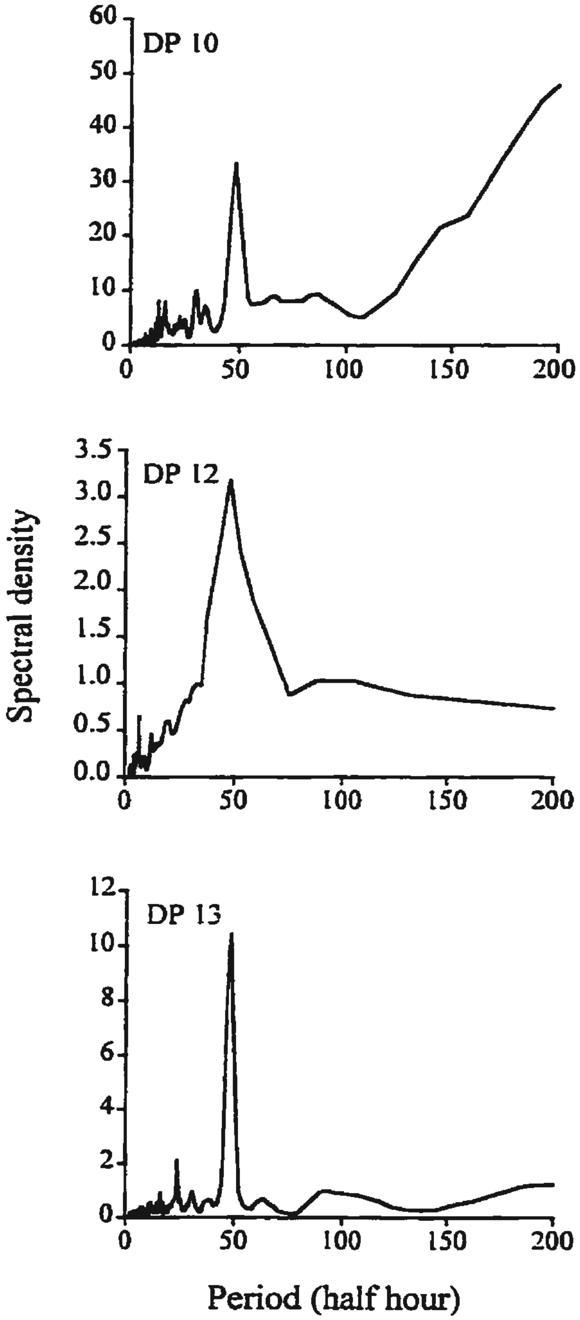

Figure F-1 (continued). Activity (TK-HH) periodograms for Babette showing peaks in spectral density generally at period 48 (DP=deployment period).

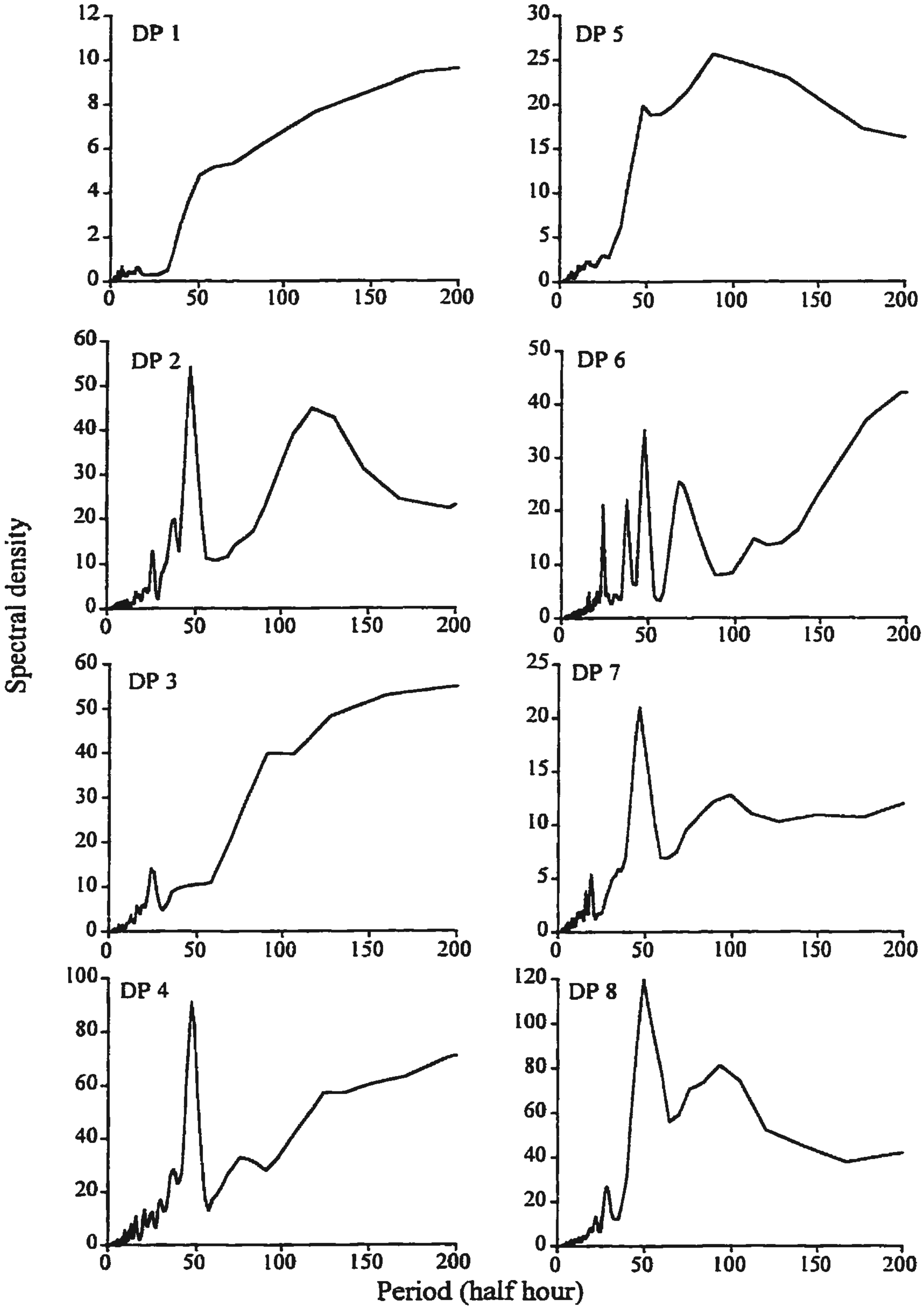

Figure F-2. Activity (TK-HH) periodograms for Chelsea showing peaks in spectral density generally at period 48 (DP=deployment period).

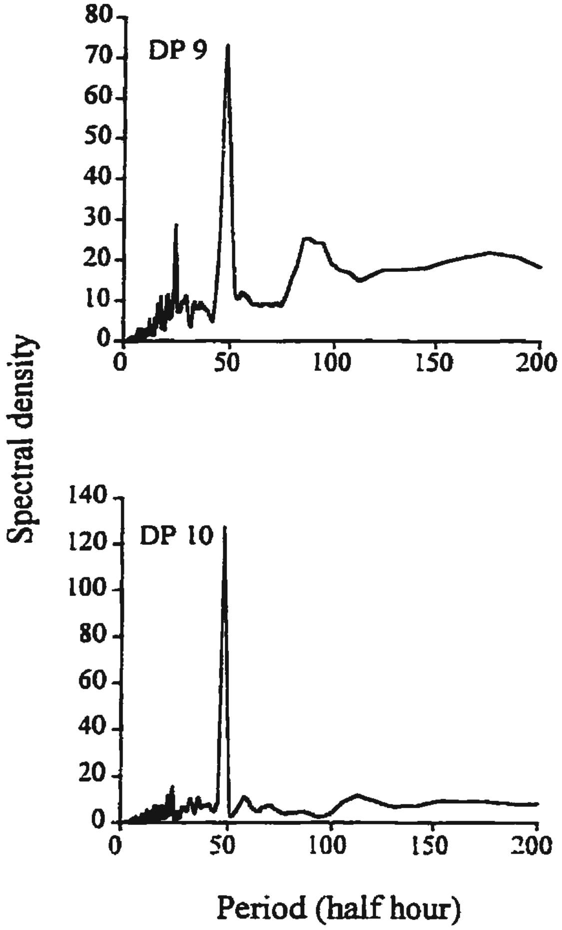

Figure F-2 (continued). Activity (TK-HH) periodograms for Chelsea showing peaks in spectral density generally at period 48 (DP=deployment period).

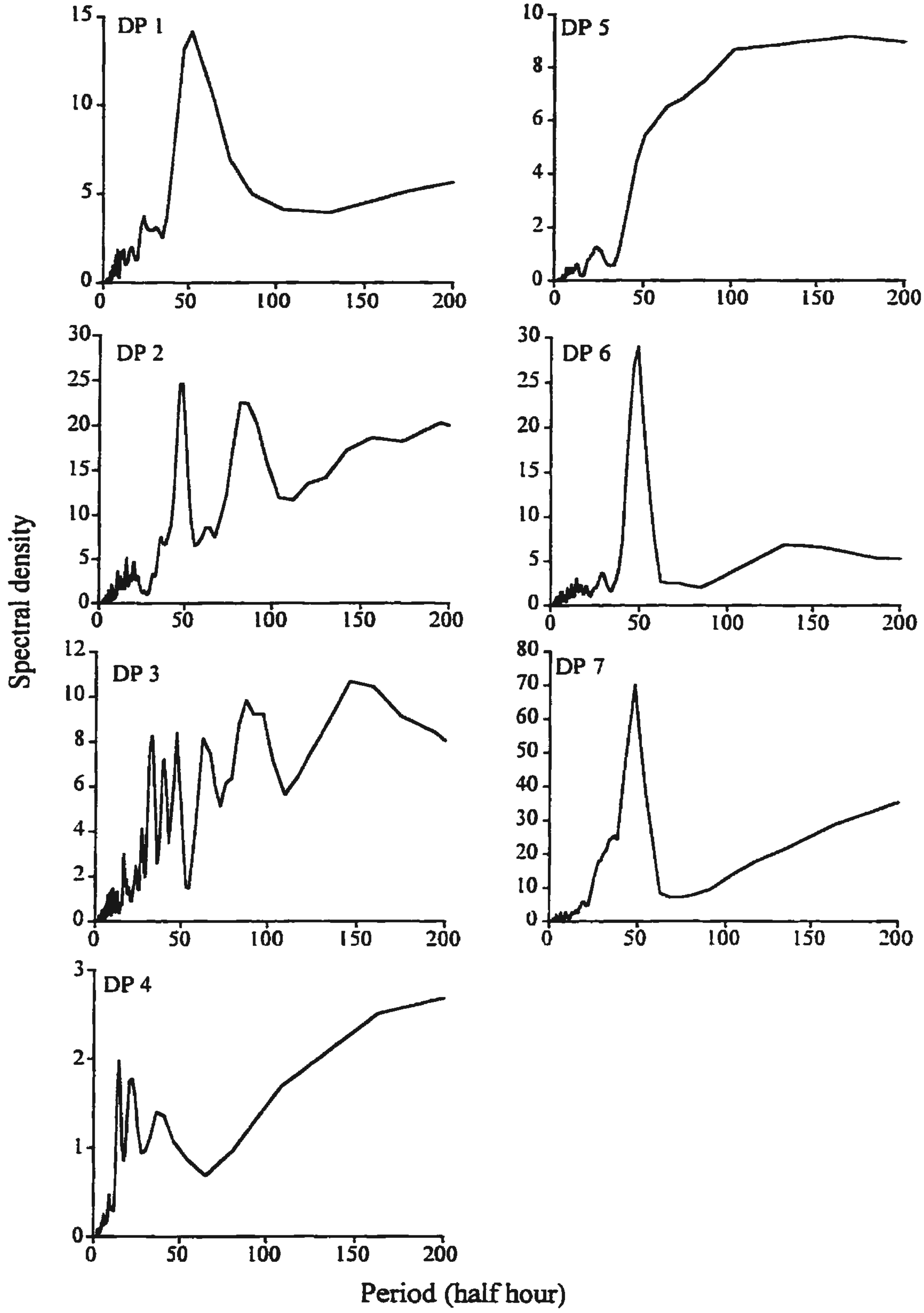

Figure F-3. Activity (TK-HH) periodograms for Elmo showing peaks in spectral density generally at period 48 (DP=deployment period).

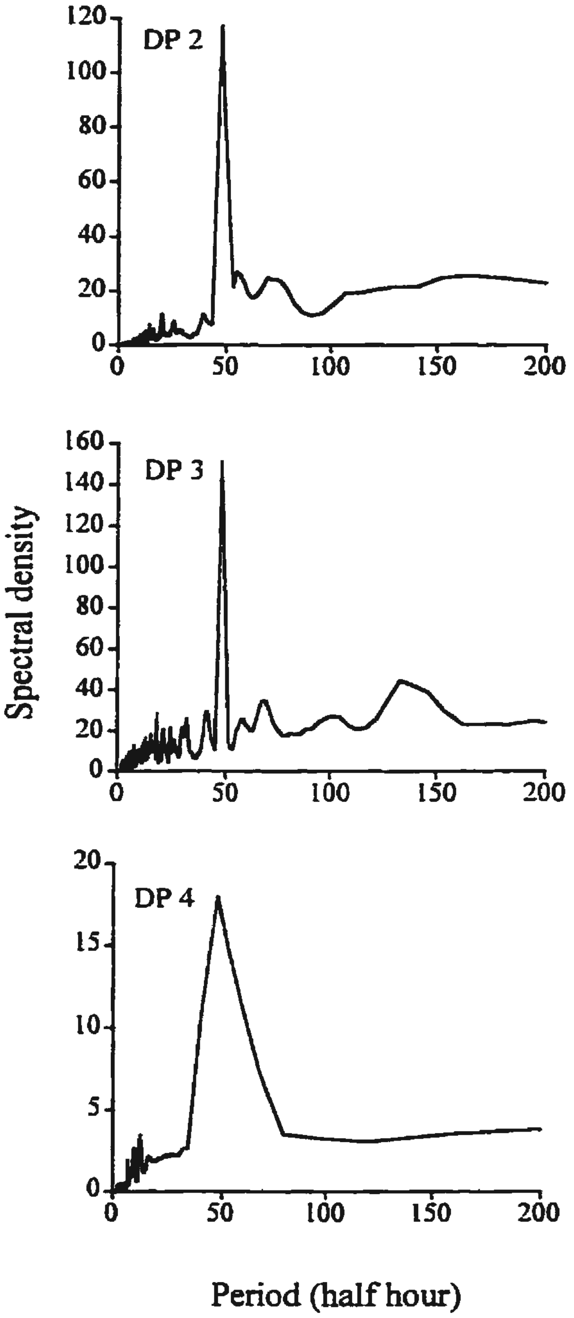

Figure F-4. Activity (TK-HH) periodograms for Jamie showing peaks in spectral density generally at period 48 (DP=deployment period).

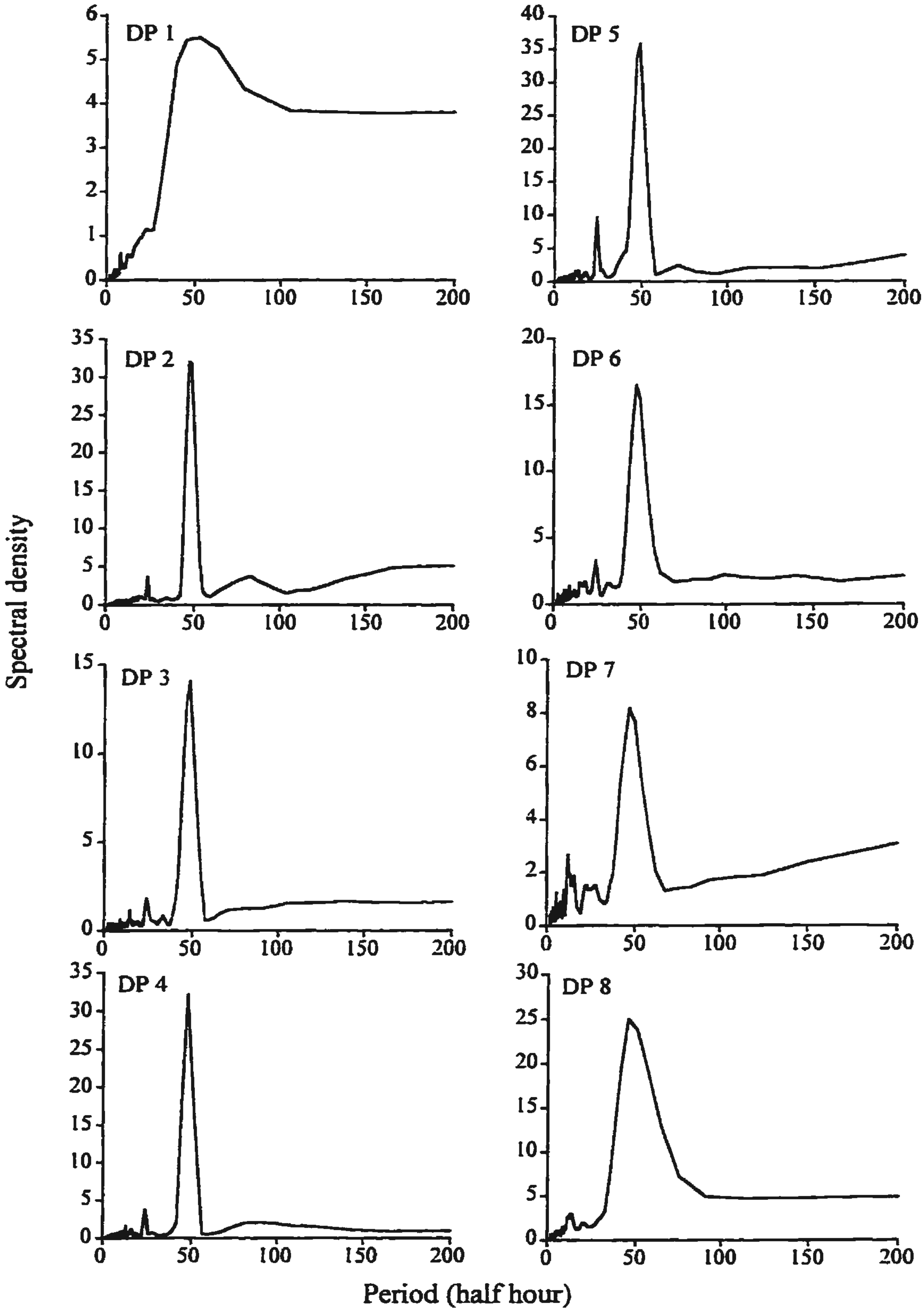

Figure F-5. Activity (TK-HH) periodograms for Mickey showing peaks in spectral density generally at period 48 (DP=deployment period).

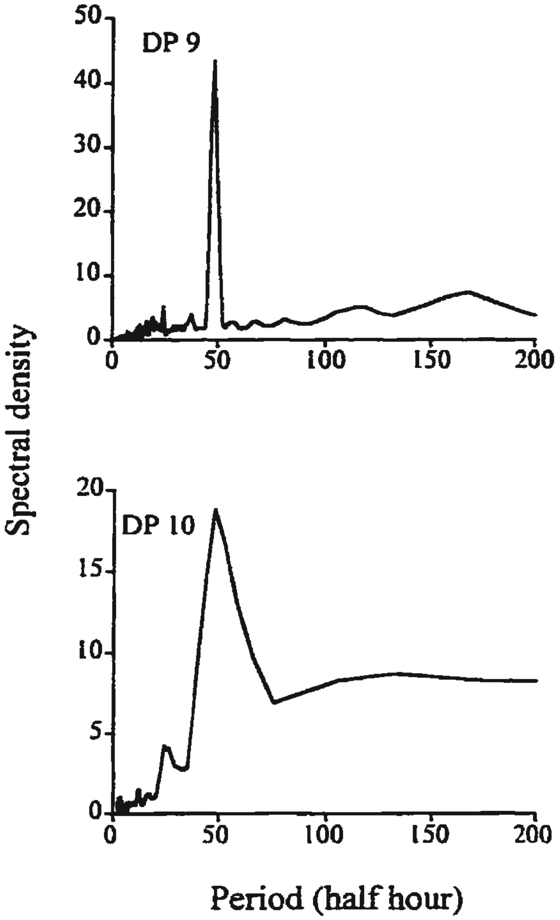

Figure F-5 (continued). Activity (TK-HH) periodograms for Mickey showing peaks in spectral density generally at period 48 (DP=deployment period).

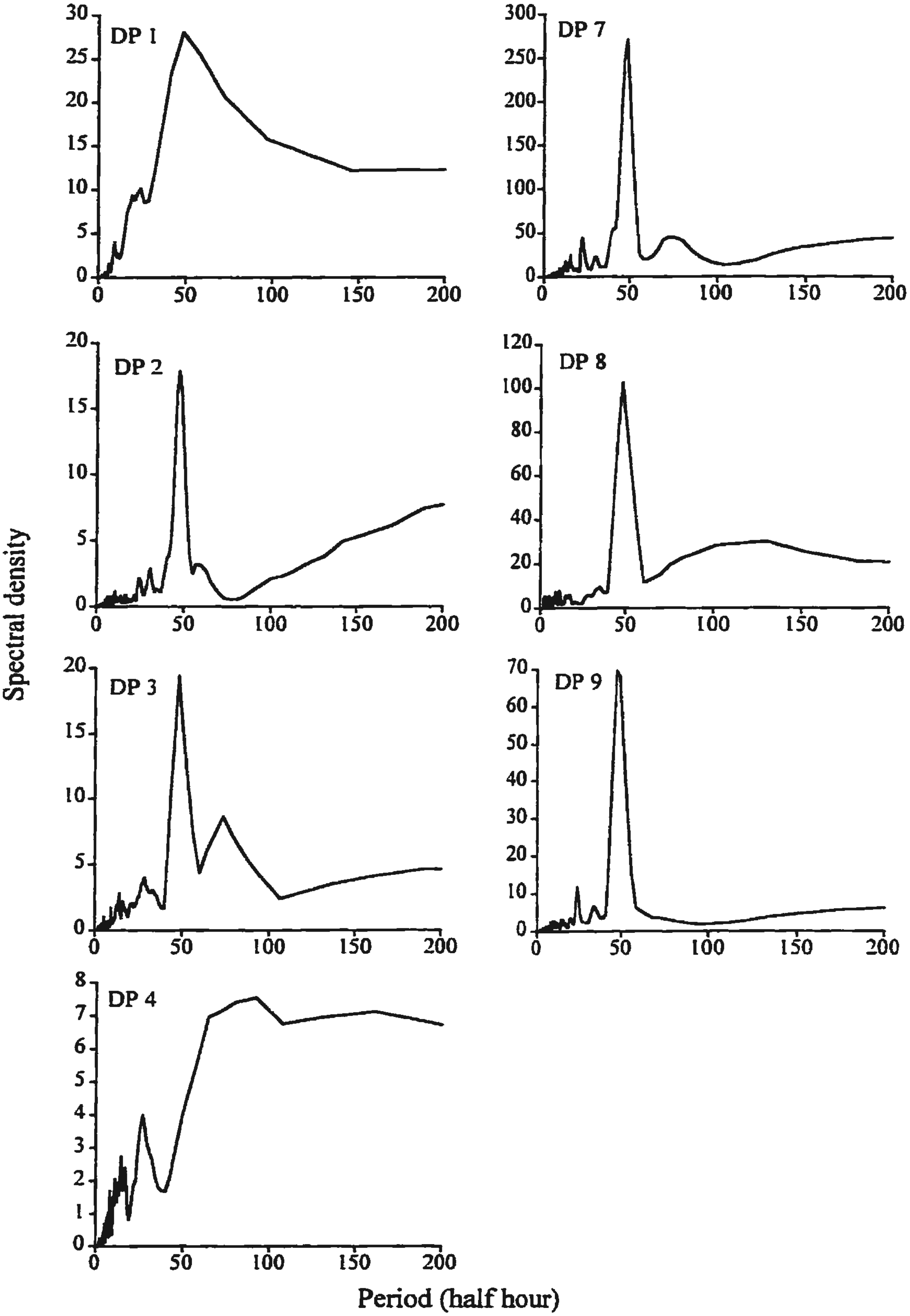

Figure F-6. Activity (TK-HH) periodograms for Rhonda showing peaks in spectral density generally at period 48 (DP=deployment period).

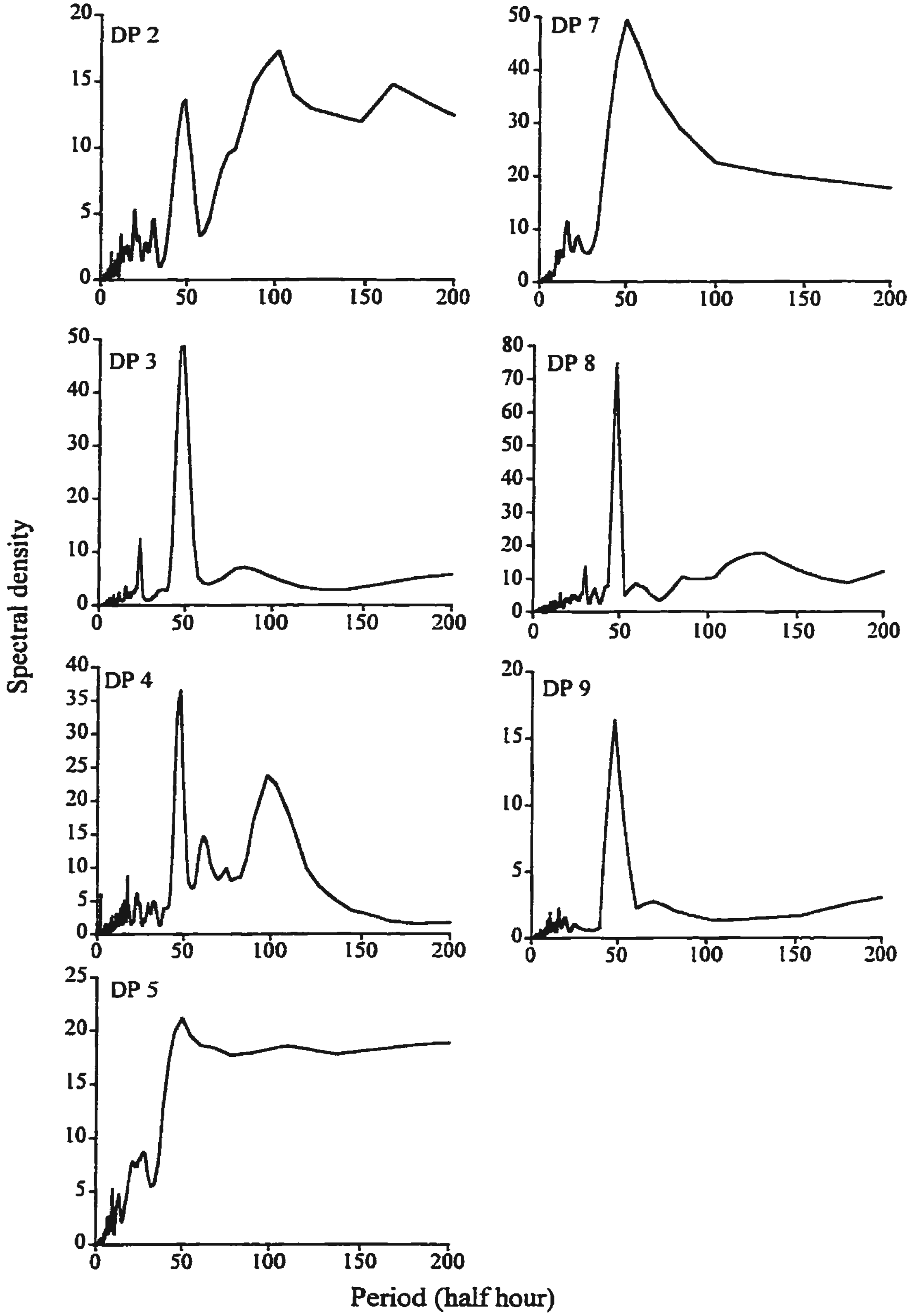

Figure F-7. Activity (TK-HH) periodograms for Tyler showing peaks in spectral density generally at period 48 (DP=deployment period).

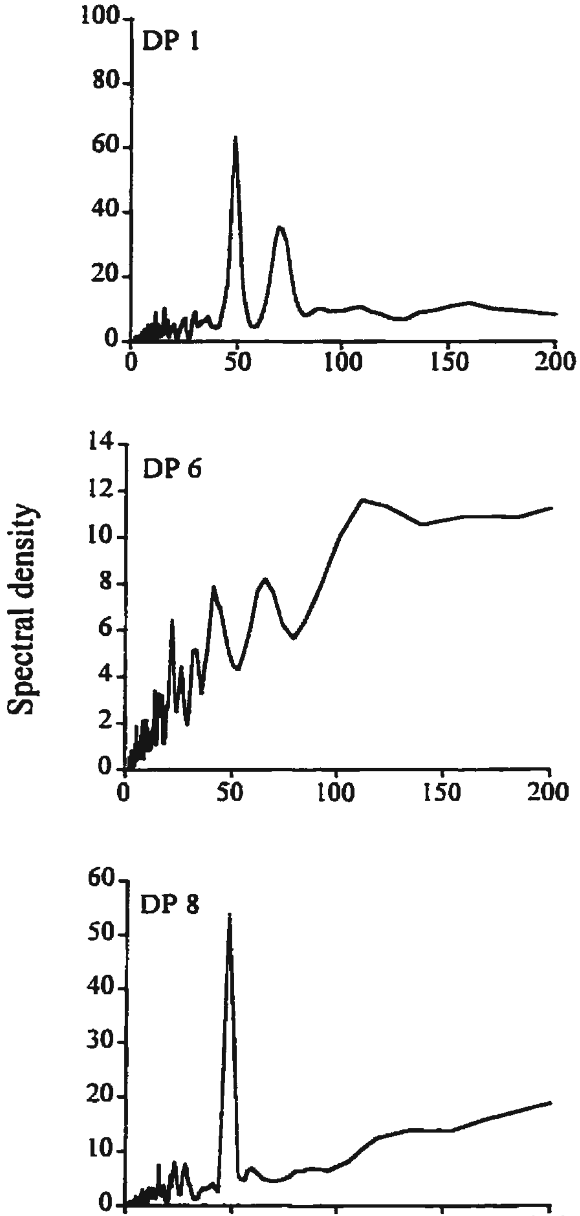

Figure F-8. Activity (TK-HH) periodograms for Victor showing peaks in spectral density generally at period 48 (DP=deployment period).

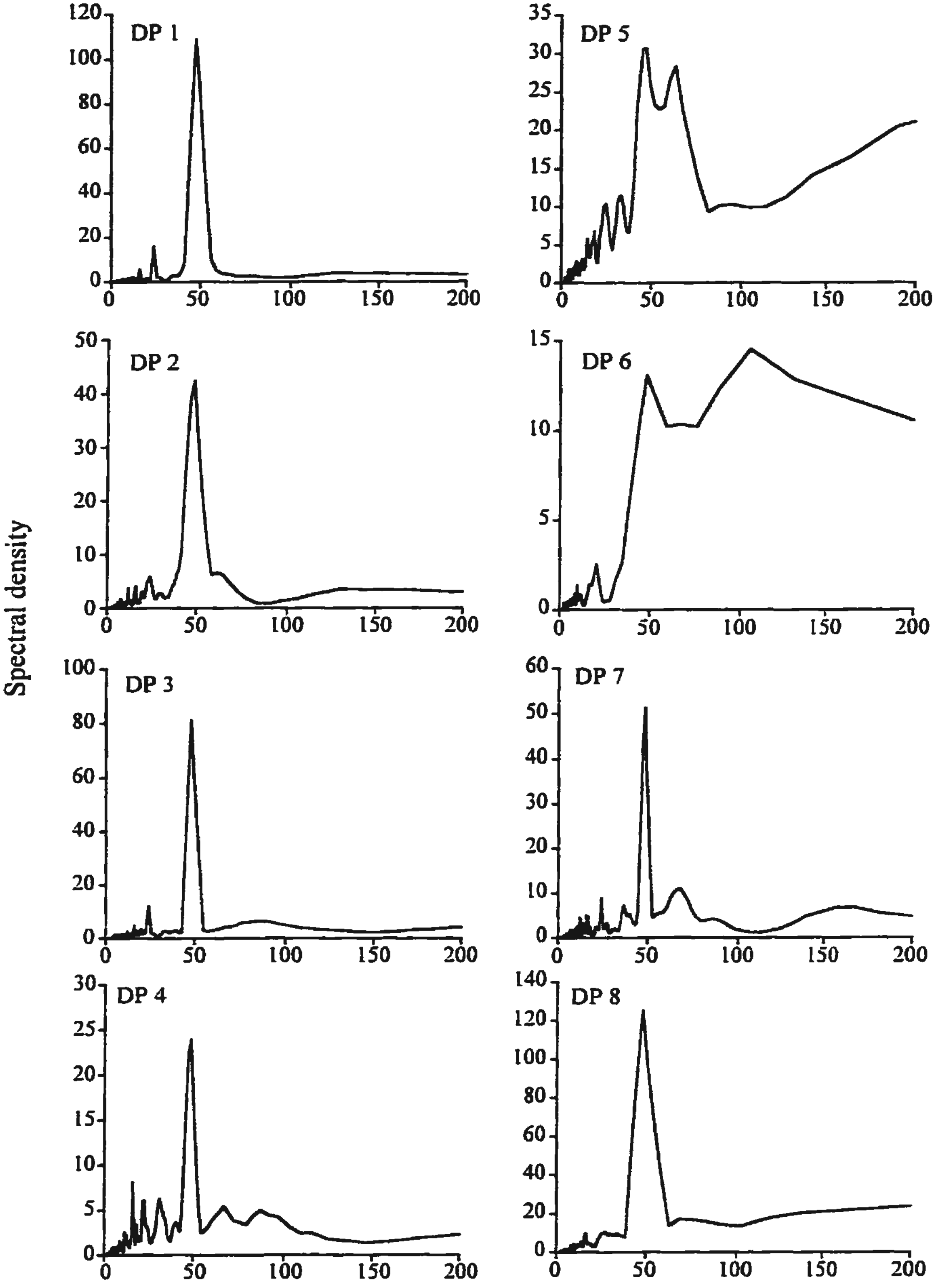

Figure F-9. Activity (TK-HH) periodograms for Virgil showing peaks in spectral density generally at period 48 (DP=deployment period).