

ELEPHANT SEAL MOVEMENTS: SOME FREQUENCY BASED STUDIES

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Summary

We studied dive patterns of northern elephant seals, that consisted of measurements of time vs. depth, by applying several time series based techniques. A primary feature of these patterns is diel variation in dive duration and maximal dive depth. Time series analysis of this variation over a two month period of continuous diving revealed an apparent circadian rhythm. The consistency of this rhythm despite large scale geographic movement during migration may suggest that the pattern is endogenous or that environmental (biotic and abiotic) factors are sufficiently similar over large ocean areas in the eastern North Pacific to

result in these consistent circadian foraging behaviors. A model involving stochastically elicited impulse responses is proposed.

Key words: Diving; Elephant seal; Fourier analysis; Marine mammal; Migration; Parallel boxplots; Periodogram analysis; Point process; Spectrum; Starplot; Time series.

1 Introduction

Data of the form $Y(t)$, $t = 0, \dots, T-1$ are studied, with t referring to times 30 seconds apart and Y the ocean depth of a migrating northern elephant seal, (*Mirounga angustirostris*). A variety of descriptive analyses are carried through employing tools of point process and time series analysis.

Section 2 describes the data and data collection procedures and mentions some of the questions that marine mammalogists think are important. Section 3 provides a brief review of stochastic models of particle movement. Section 4 presents time series and point process periodogram analyses and some other studies of the data. Section 5 sets down one formal model suggested by the situation. There is discussion of the work and results in Section 6.

This paper focusses on the case of a real-valued time series (depth). Others in a series of papers, (Brillinger(1996), Brillinger and Stewart (1996a)), are concerned with the bivariate case (of latitude and longitude).

2 The data and some descriptive statistics

The primary data set for marine vertebrates that is studied here is for the northern elephant seal (*Mirounga angustirostris*). This species breeds on offshore islands and at a few mainland sites along the coasts of California

and Baja California (Stewart and Huber, 1993; Stewart et al., 1994). Adults are ashore briefly in winter to breed and again in spring (females) or summer (males) to molt but spend the remainder of the year, 8-10 months, at sea foraging. They each make two precise, long-distance migrations each year between islands in southern California and offshore foraging locations in the mid-North Pacific, Gulf of Alaska and along the Aleutian Islands covering 18,000 to 20,000 km (surface movements alone) during the double migrations (Stewart and DeLong, 1995). The seals dive continually during these migrations. The dives average 20 to 40 minutes long (longest = 2 hours) and 350 to 650 meters deep (deepest = 1560 meters) and are only separated briefly for 2-3 minutes while the seals are at the sea-surface breathing (e.g., DeLong and Stewart, 1991; Stewart and DeLong, 1995). See Figure 1 for the track of one migration and the record of six successive days of diving. In the top graph a great circle path has been superposed for reference.

The data studied refer to vertical movements, recorded at 30 second intervals, throughout the period at sea by a microprocessor-controlled event-recorder which was harmlessly glued to an elephant seal's hair at San Miguel Island off Southern California (e.g., Stewart and DeLong, 1995; Bengtson et al., 1992; Stewart et al., 1989). The instrument was attached at the end of the breeding season and then recovered when the seal next returned to shore several months later to molt. Stored data (hexadecimal format) were then downloaded from the recovered instruments and converted into time-depth binary form.

The diving behaviors of these seals are of great theoretical and empirical interest to biologists because when at sea seals must effectively balance their time foraging at relatively great depths where prey concentrate,

with time at the sea surface to breathe and to store sufficient oxygen in blood and tissues to support the next dive. During foraging periods at sea, each lasting several months or more, the seals must recover substantial body mass that was lost when inshore and fasting during the breeding (1-3 months) and molting (1 month) seasons. Moreover, they must acquire additional nutrients as energy to support growth and gestation and to store sufficient depots of fat to support the next period of terrestrial fasting. But proper interpretations and assessment of intra and inter-individual differences in these complex diving patterns related to biotic and abiotic variability require more than simple statistical description. A holistic approach of statistical analysis that can both describe and account for variability in these behaviors is needed as a basis for exploring models of foraging efficiency vs. physical and physiological constraints (eg., Boyd and Croxall (1996), Carbone and Houston (1996)).

Figure 2 presents a star plot of the whole time series of $T = 215895$ observations. The value at 12 o'clock corresponds to $t = 0$. The successive values of $Y(t)$ are laid down in counterclockwise manner with the distance from the center corresponding to the depth. This sort of plot appears convenient for bringing out certain aspects of very long time series. This journey is seen to start with some shallow dives. One notices some bands of avoided depths.

Figure 3 is another way to present the data. What is provided in this figure is a series of parallel boxplots for each day. Again one sees shallow dives at the start. On day 85 the seal spends an unusual amount of time at and near the surface. When one looks back to the star plot one notices that day there as well. The dives are shallow at the end. The median dive depth is remarkably stable. For Day 119 one notices a

scattering of extra deep dives.

Simple examination of the series $Y(t)$, $t=0,\dots,T-1$ does not immediately bring out some important aspects such as possible presence of a circadian (i.e. approximately 24 hour period) rhythm or of slowly changing characteristics. These will be elicited below by particular techniques.

3 Some formal descriptions

The Langevin equation is often used to describe the motion of particles. It may be written

$$\frac{d^2\mathbf{r}}{dt^2} = -\beta\frac{d\mathbf{r}}{dt} + \frac{d\mathbf{B}}{dt}$$

with \mathbf{r}_t position at time t , β a coefficient of resistance and \mathbf{B}_t Brownian noise. In the equation, the \mathbf{B} term can be viewed as representing the seal's foraging. A discrete approximation to such an equation and the inclusion of measurement error leads to the consideration of ARMA models. However, because of the impulsive character of the series shown for example in the bottom graph of Figure 1, one cannot expect an such a model to be particularly appropriate.

An external force term, $\mathbf{F}(d\mathbf{r}/dt, \mathbf{r})$, might be added to the righthand side of the equation for a more realistic model. For example one might consider basing a model on a linear time invariant system representation. In the present case one could set up a series of dive start times, say setting $X(t) = 1$ if a dive starts at time t and $X(t) = 0$ otherwise. Then one could consider the model

$$Y(t) = \sum_u b(t-u)X(u) + noise$$

for example. This model now presents impulsive behavior; however

examination of the bottom graph of Figure 1 suggests that the impulse response $b(\cdot)$ varies from dive to dive.

4 Results of some analyses

The total record studied has length 215985 points, and the depth measurements are spaced 30 seconds apart. The record consists of dives interspersed with time spent at the surface, (depth = 0, see the bottom graph of Figure 1.)

4.1 Periodogram analysis

4.1.a Full series

To begin, the periodogram of the entire record was computed, that is

$$\frac{1}{2\pi T} \left| \sum_t Y(t)e^{-i\lambda t} \right|^2$$

for $\lambda = 2\pi s/T$, $s = 1, \dots, T/2$. The result is displayed in Figure 4. The top graph presents values for frequencies below 2.66 cycles per day. One sees a pronounced peak at 1 cycle/day and also its first harmonic at 2 cycles/day. These frequencies correspond to a diel pattern and a circadian rhythm. One also sees increased power at very low frequencies. This could relate in part to the inclusion of shallower dives at the beginning and end of the migration. The width an approximate 95% confidence interval is indicated by the vertical line on the figure.

The lower graph refers frequencies up to the Nyquist limit of 1 cycle per minute. Because of the ranges of the quantities involved the relationship is plotted in log-log fashion. One sees the second harmonic of the daily cycle. Also apparent are broad peaks around 50 and 100 cycles/day. These can be associated with the generally regular behavior of about 2–3 dives/hour. This point will be returned to below.

4.1.b The point process of dive starts

The times of dive starts were fairly clear in the original record and are studied next. Suppose they are denoted by $\{\tau_j\}$. The periodogram of a stretch of point process values is defined as

$$\frac{1}{2\pi T} \left| \sum_j e^{-i\lambda\tau_j} \right|^2$$

and is useful to detect the presence of periodicities. Figure 5 provides this function for the point process of dive start times. The daily cycle is strong once again, but the first harmonic no longer stands out. This absence suggests that the harmonic results from the character of the depth values, rather than the times of dive starts. Approximate 95% confidence limits are indicated by the vertical lines.

4.2 The daily component

The previous analyses strongly suggest the presence of a circadian component. To learn something of its character one can graph boxplots for successive hours of the day, Figure 6. One sees, for example, that dives are generally deeper midday and shallower around 6-7 am. Also there is a smooth transition between the hours. Hour 7 shows the extreme dives also apparent on Day 119 of Figure 3. Figures 3 and 6 provide an interesting decomposition of the series.

4.3 Phase of the daily component

As seen in the top graph of Figure 1, the animal travels a substantial distance in a west by northwest direction and then returns home. One wonders about picking up a phase change in the 24 hour component, resulting from this movement. The animal's journey involves three different time zones. One might have expected the phase plot to show a line

with a positive slope for the first half and a negative slope for the second half, given the motion of the sun.

Suppose one envisages a cosine plus stationary noise model for each day. Figure 7 graphs the estimated phase angle of the 24 hour component for the successive days. This estimate is obtained by ordinary least squares. Its variance is approximately $2\pi f_{\varepsilon\varepsilon}(\alpha)/(4\pi\rho^2V)$ where $f_{\varepsilon\varepsilon}$ is the background noise spectrum, $\alpha = 2\pi/2880$, ρ is the amplitude of the component and V the number of observations made in a day. Robust smooth line has been added to the figure for reference. If there is a phase change it appears too small to be picked up by the present method, although the standard error estimate provided by the above formulas is .005.

The lower graph is the estimate $\hat{\rho}$. A smooth curve has been superposed for reference. The amplitude appears to be increasing as time is passing, i.e. the 24 hour component becoming stronger. This could also be due to the dives becoming relatively deeper as time passes too.

Figure 9 provides an example of a day's dives and the fitted 24 hour cosine function.

4.4 Dive sequences

The periodograms of Figure 4 show peaks at periods of 24 and 12 hours. In order to better understand the shorter period behavior the series was broken into successive 12 hour segments. The average of the segments' periodograms, separately for before noon and after noon time, is shown in Figure 10. The humps around 50 and 100 cycles per day are characteristic of phenomena driven by approximately regular renewal processes for example. Noting the sharpness of the peaks in the bottom graph of Figure 8 one can infer that the after noon diving is more regular.

The background noise in appears to fall off, on these log-log plots, approximately in linear fashion. This is a characteristic of $1/f$ noise and will be investigated in future work.

The bottom graph of Figure 1 shows that 300 successive dives vary noticeably amongst themselves. Figure 10 shows the result of superposing the successive individual dives. One sees substantial variation in the depths and the lengths of the dives. This phenomenon is investigated in more detail in Brillinger and Stewart (1996b).

4.5 Bispectral analysis

By inspection of the bottom graph of Figure 1 one sees that the data are quite nonGaussian. This suggests that bispectral techniques might be of use. For example one can ask if the dive series, showing a broad component of frequency around 50 cycles/day, is tied in with the daily cycle. The dives do appear deeper at early afternoon. The bispectrum is one tool to address this question. One needs a variant capable of handling interaction between a discrete component and a broadband one. Munk et al. consider such a problem for the interaction of tidal frequencies and the very low frequency band. One would see, in Figure 4, the hump at 50 cycles/day displaced to 50 ± 1 cycles/day. Such an occurrence is not apparent in the present plots, perhaps because of lack of resolution. The question is possibly better investigated via the bispectrum and bicoherence. This will be done in future work.

5. A model

The previous discussions suggest consideration of a particular model.

Let $N = \{\tau_j\}$ correspond to the point process of times at which dives start. (The periodogram of its realization is given in Figure 5.) Suppose

that dive shapes are sampled from a distribution, and realizations written $a(u; \omega)$, $u = 0, \dots, U$ with ω indexing realization. (The curves of Figure 9 are representative.) Let $A(\lambda; \omega)$ denote the Fourier transform of $a(u; \omega)$ and let

$$b(u) = E_{\omega}\{a(u; \omega)\}, \quad B(\lambda) = E_{\omega}\{A(\lambda; \omega)\}$$

be the corresponding expected values.

Consider representing the time series of depths by

$$Y(t) = \sum_j a(t - \tau_j; \omega_j)$$

with ω_j representing the realization occurring for the j -th dive. A switching between dive shapes is taking place. Then assuming $\{\tau_j\}$ independent of $\{\omega_j\}$

$$E\{Y(t) \mid N\} = \sum_j b(u - \tau_j)$$

This is a linear time invariant model amenable to cross-spectral analysis, see Brillinger (1974). Further, if the process N is stationary and the ω_j are i.i.d., the power spectrum of the process Y is given by

$$f_{YY}(\lambda) = f_{NN}(\lambda) |B(\lambda)|^2 + \frac{c_N}{2\pi} |C(\lambda)|^2$$

with $|C(\lambda)|^2 = \text{var } A(\lambda; \omega)$, c_N the rate of the point process and f_{NN} its spectrum.

The shape of the periodogram in Figure 4 can be thought of as mimicking this formula, once one notes Figures 5 and 8. The 24-hour component of the point process N , and the shape of Figure 8, are apparent. The second harmonic is not however. In part this must be due to the fact that the apparent difference between the before noon and after noon dive

depths is not included in the model.

6 Discussion

The work presented shows that thinking in frequency domain terms can shed light on data of the type considered here. In particular, the presence of a circadian rhythm has been elicited and studied in several fashions. Future work will include repeating these analyses with other animals.

The work has proceeded by deriving various quantities, from the original series, and studying them in their own right. It is fortunate that there is a lengthy series to work with. The various plots lead to noting particular features to focus on.

Figures 7 and 8 suggest that $a(u;\omega)$ depends on the time of day. Also, serial correlation turns out to be present in the series of successive dive types and is studied in Brillinger and Stewart (1996b).

Figure 9 makes one think of evoked response analysis, for which many statistical techniques are available (see eg. Brillinger (1981)). Other interesting questions concerning data of the type studied here may be found in Testa (1993).

Diel patterns in dive depth and dive duration appear to be characteristic of northern (eg. DeLong and Stewart (1991), Stewart and DeLong (1995)) and southern (eg. Junkel and Bester (1994)) elephant seals. Our analyses of these diving patterns using several time series models has demonstrated a consistent circadian pattern in the northern elephant seal despite the seal's movement over a large area of the eastern north Pacific during a 74 day-long foraging migration. This temporal consistency in the circadian pattern suggests that it may be endogenously controlled or, alternatively, that the abiotic and biotic environmental factors may be

sufficiently consistent over this broad oceanographic spatial scale to constrain such behavioral patterns. No mechanism is obvious for the former but the latter hypothesis is testible by sampling the physical and biological environment along the typical migrating routes and vertical habitats used by foraging northern elephant seals.

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Legends

Figure 1. The top graph provides the estimated mid-day positions of the migration of a seal in 1991. The bottom graph is the continuous record of depth over a six day period. The days are stacked under each other, from first to last.

Figure 2. A star plot of depth for the entire migration. The values are laid down, starting at the top, and moving counter-clockwise.

Figure 3. Parallel boxplots for each day's observed depths. The vertical scale is in meters.

Figure 4. The periodogram of the time-depth data. The top figure is the lower frequency band only. The bottom figure provides the complete periodogram. The vertical line indicates an approximate 95% confidence interval.

Figure 5. As for Figure 4, except the periodogram for the point process sequence of dive start times.

Figure 6. Boxplots for each hour of the day. The center dot in each box is the median. The ends of the boxes give the upper and lower quartiles. The hour is Pacific Standard Time (PST).

Figure 7. An estimate of the phase angle and amplitude of the 24 hour component for each day of the migration. A smooth lowess curve has been superposed on each.

Figure 8. The dives for day 127 with fitted 24 hour component superposed.

Figure 9. The average of the periodograms of successive 12 hour segments, separately by before and after noon PST.

Figure 10. Three hundred successive dives overlaid.