Elephant Seal Movements: Dive Types and Their Sequences *

David R. Brillinger   Brent S. Stewart

Department of Statistics
University of California
Berkeley, CA

Hubbs-Sea World Research Institute
San Diego, CA
and
Boalt Hall School of Law
University of California
Berkeley, CA

ABSTRACT
This paper is concerned with time-depth curves recorded for northern elephant seals that are migrating. The curves show a succession of dives of varying depths, durations and types. A mixture model is employed to estimate the various curves present. An advantage of this procedure, over the ones that have been employed, is that it is automatic. Further a categorical-valued series is developed for the sequence of dives. It is examined for evidence of independence for both dives of one type and amongst dives of different types.

Key words and phrases: Categorical-valued time series, dive patterns, elephant seals, foraging behavior, longitudinal data; mixture model.
AMS 1991 subject classifications: Primary 62M10; 62M15; 62P10.

1 Introduction

Studies of the foraging behaviors of a variety of marine vertebrates (eg. seals, sea lions, penguins, sea birds, sea turtles) have been conducted in recent years using micro-processor controlled event recorders to document diving patterns. The data generated from these recorders are time series

*The work of DRB supported by the Office of Naval Research Grant N00014-94-1-0042 and the National Science Foundation Grant DMS-9625774. Elephant seal dive data were collected in previous studies with partial support of a contract to BSS from the Space and Missile Command, U.S. Department of the Air Force.

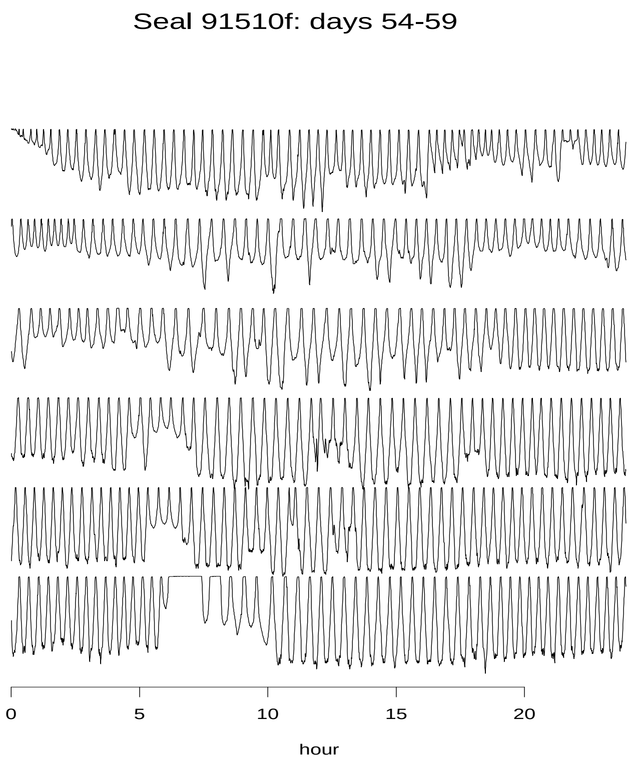

FIGURE 1. Six days diving for one seal. The curves from top to bottom represent the seal's depth as a function of hour for six successive days. Depth was measured every 30s.

of depth measurements made at regular intervals (5s to 60s) over days to months. These data are often displayed graphically as two-dimensional plots of depth versus time. Consequently the two-dimensional shapes of dives, which lack spatial components (i.e.latitude and longitude), have been described and used to separate them into discrete categories of similar shapes, sometimes according to maximum depths reached and durations of dives. For the most part, the dives have been classified into a small number of shape categories by visual inspection (eg. [1], [10], [17], [20], [9], [22], [26], [27]).

The function (eg., swimming, hunting, exploring) of various dives have been inferred from their two dimensional shapes. Further, the inferred functions have been incorporated into discussions of animal physiology and energetics. Thus, the ability to classify dives according to shapes based on time and depth interactions has had utility in developing hypotheses about foraging strategies and efficiency in free-ranging aquatic predators.

Using time-depth series collected for foraging northern elephant seals (*Mirounga angustirostris*). We earlier developed, [8], a computer-assisted method to automatically and quickly describe dive shape with an algorithm to fit joined straight line segments employing the BIC criterion to estimate the number of segments. Here we develop an alternate approach.

As in other species studied, the individual dives of northern elephant seals seem to consist of a restricted number of types, possibly indicating different activity and function (see Figures 1 and 2). In addition to basic questions and inferences of function of particularly shaped dives, it is important to assess the patterns of sequences and mix of the various types to explore hypotheses concerning navigation and orientation, sleep, predator avoidance and the influences of geographic location on foraging strategy.

The data studied in the paper may be seen as curves or segments stretched one after the other. Experiments in which the basic data are curves have been studied in various ways, see [2], [3] and the references therein. One technique is principal components, see [15], [24]. Others are presented in [18] and [28]. In particular, longitudinal data analysis and modelling are discussed in the books [13], [19] and [14]. The data of this paper differ from the usual longitudinal data in that there is but one subject (here a seal) and the curves run one after the other. These data are of the character of the response in an evoked response experiment, see [4].

The observations of discrete categories of two-dimensional shapes of types leads to consideration of a mixture model involving particular functional forms occurring with particular probabilities. That having been said, the model considered in this paper is: the data are curves with $Y_j(u)$ referring to the seal's depth u time units after the start of the j-th dive. The variate $Y_j(u)$ has conditional expected value $a_k(u)$, with probability $P_k,\ k = 1, \ldots$ indexing the types.

After this model has been fit, one can go on to estimate the type, k, of a particular dive, and thence obtain a sequence of dive types, $\hat{k}_1,\ \hat{k}_2,\ \ldots$. This categorical-valued time series can be examined for short and long range temporal dependence for example.

Some details of the data are provided in Section 2. Section 3 indicates the fitting procedure employed to obtain estimates of the various dive types. The results of this fitting are presented in Section 4. The next section refers to the sequence of dive types and presents the results of analyses looking for serial dependence. Section 6 provides discussion, particularly of the problem of identifiability, and summary.

There are three other papers concerned with the data for this particular seal, [5], [6], [7].

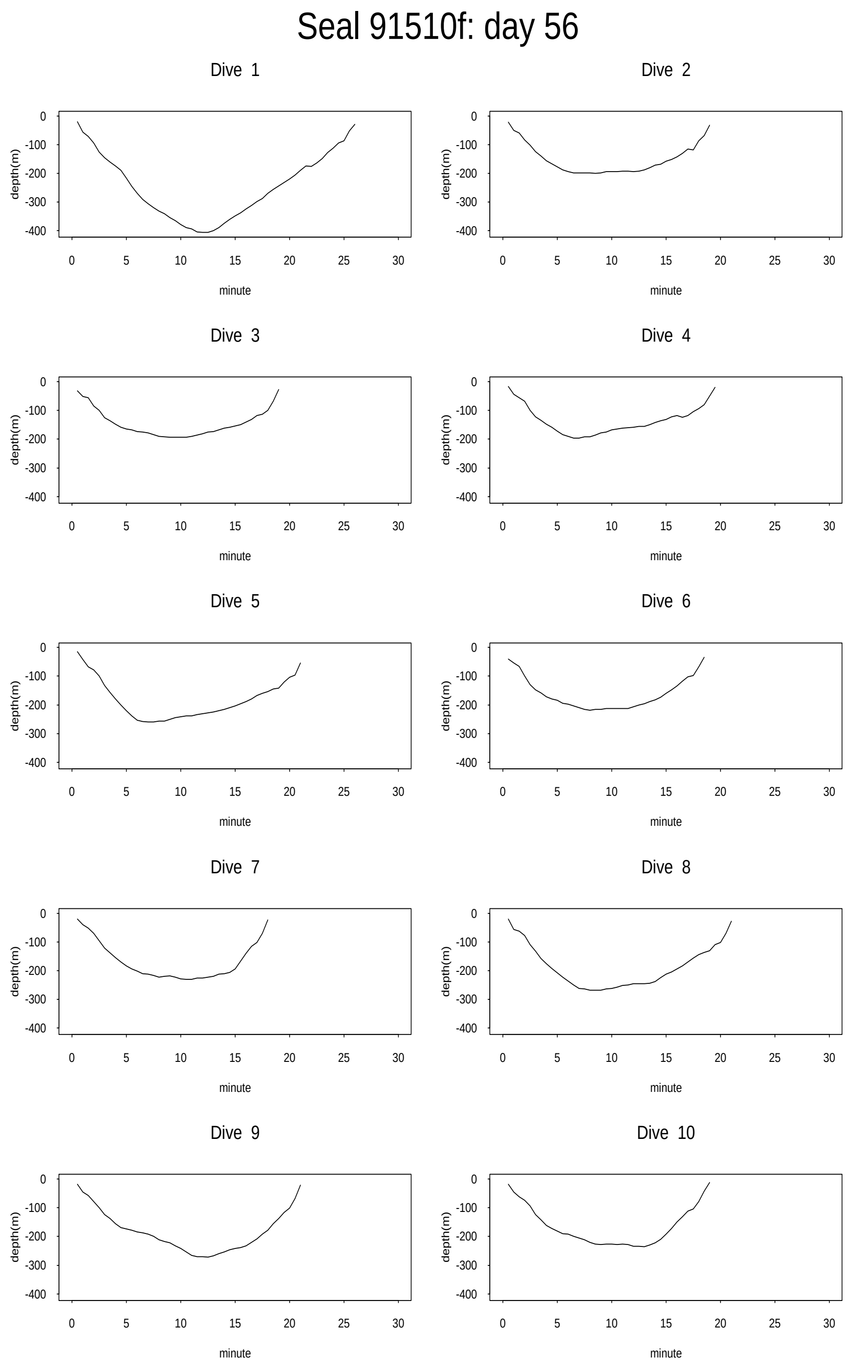

FIGURE 2. The first 10 dives of Day 56.

2 The Data

The data set analyzed in the present work is for a female 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 ([30], [32]). 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 make two solitary, 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 ([29]). The seals dive continually during these migrations; 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., [12], [29]). The data studied here are depth measurements made at 30 second intervals throughout the periods at sea (See Figures 1 and 2.) They are recorded by a microprocessor-controlled event-recorder which is harmlessly glued to a seal's hair (e.g.[29], [1], [31]). The instruments are attached at the end of the breeding or molt season and then recovered when the seals next return to shore several months later.

The dives' start times could be read from the time-depth record quite clearly allowing individual dives to be selected, as graphed in Figure 2 for example.

3 Fitting a Mixture of Dive Types

Let $Y_j(u)$ denote the depth at lag u in j-th dive. Suppose there are possible types $a_k(u),\ k = 1, 2, ...,$ with k to be selected randomly. One may consider the model:

$$Prob\{K = k\} = P_k \tag{1}$$

$$Y_j(u) = a_K(u) + \epsilon_j(u) \tag{2}$$

for $k = 1, 2, ...$ and $j = 1, 2, ...$ with $\epsilon(.)$ representing noise. Equations (1), (2) provide a mixture model.

EM algorithms are often a convenient way to obtain maximum likelihood estimates in such models, see [11], [23], [25]. In the case that the noise values, $\epsilon(.)$, are assumed independent with variance $\sigma^2(u)$ at lag u and Gaussian, an EM algorithm for estimating the $a_k(u)$ is implemented by the recursion

$$\hat{a}_k(u) = \sum_j Y_j(u)\, \hat{p}_{jk} \ / \sum_j \hat{p}_{jk} \tag{3}$$

$$\hat{\sigma}(u)^2 \;=\; \sum_j \sum_k \; (Y_j(u) \;-\; \hat{a}_k(u))^2 \hat{p}_{jk} \;/\; J \tag{4}$$

$$\hat{P}_k \;=\; \sum_j \; \hat{p}_{jk} \;/\; J \tag{5}$$

$$\hat{p}_{jk} \;=\; \hat{P}_k \; exp\{-\sum_u (Y_j(u) \;-\; \hat{a}_k(u))^2 \;/\; 2\hat{\sigma}(u)^2\} \;/\; C_j \tag{6}$$

where C_j is determined so that $\sum_k \hat{p}_{jk} = 1$. The development of such algorithms is indicated in [25].

4 The Estimated Types

Days 56 to 115 of the migration were studied, accounting for 3629 dives. In employing the EM algorithm, starting values are needed. Here the number of dive types for the analysis was taken to be 9 and the initial curves $\hat{a}_k(.)$ were taken to be the averages of the curves in the 9 cells determined by cross-classifying by duration and depth using the 33 and 67 percentiles as the cut points of those variables. The initial values of the $\hat{P}_k$ were 1/9. Apparent convergence occurred quickly.

Figure 3 provides the results of fitting the mixture model. It is interesting that the curves obtained are all unimodal. The first and second curves each occur about 23 percent of the time. The curves may be distinguished from each other by characteristics such as: duration, maximum depth, symmetry, flatness at maximum depth.

In future work other means of generating initial curves will be investigated. Also the number of dive types might be estimated employing the BIC criterion.

5 Categorical-valued Time Series of Types

Suppose that dive types are well-defined and the actual types are given by k_j, $j = 1, 2, \ldots$. This is a categorical-valued time series. One can ask for example: Is the series k_j white noise and if it is not, how might it be described?

In practice one needs to estimate the k_j. A simple procedure is to determine for which shape, $\hat{a}_k(u)$, the j-th dive, $Y_j(u)$, has the smallest mean-squared error. The corresponding categorical-valued series was constructed. For example the estimated types for the 10 dives of Figure 2 are respectively 8, 5, 5, 5, 5, 5, 5, 5, 5, 5 . This constancy may be seen at the start of the second curve in Figure 1.

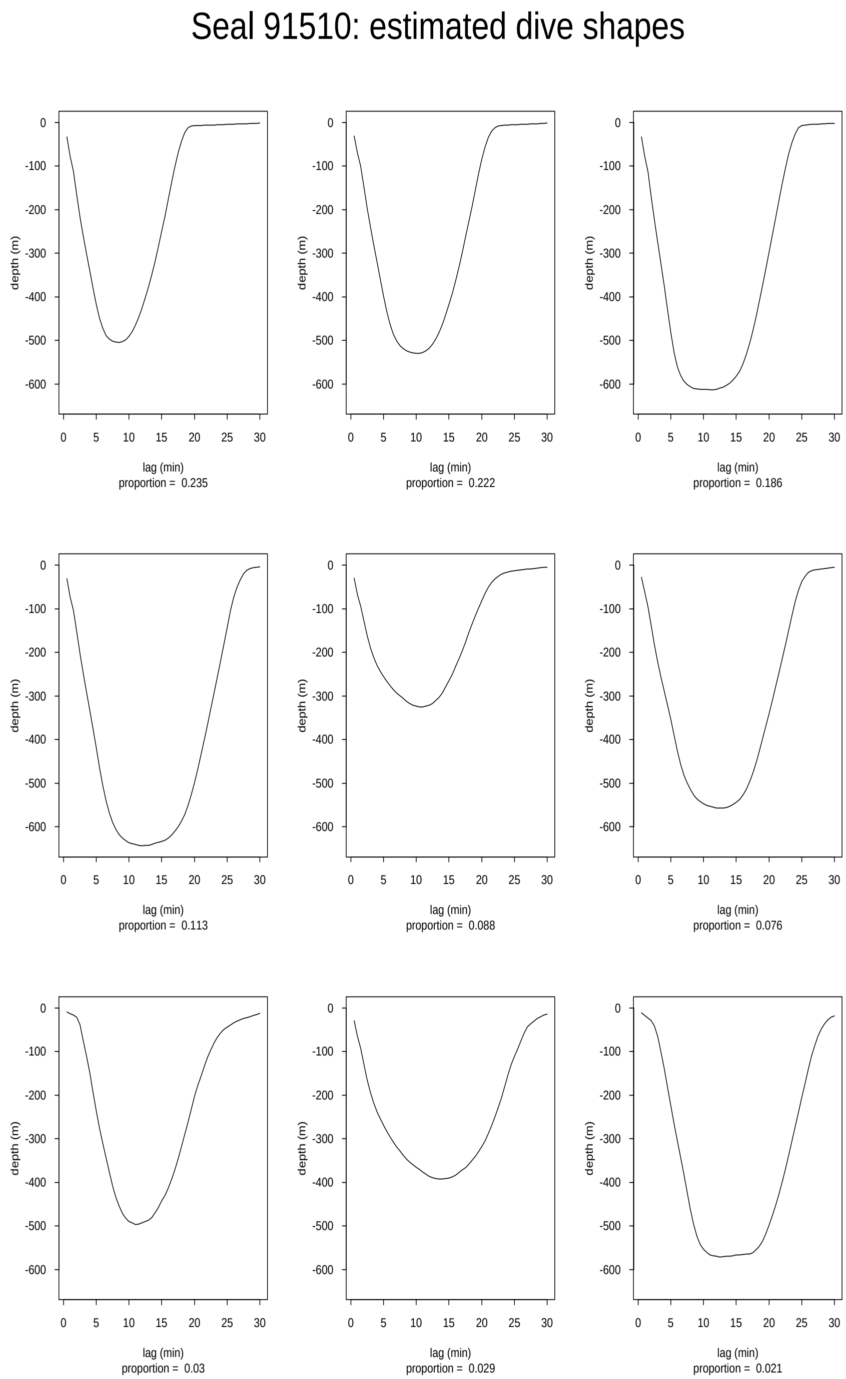

FIGURE 3. The 9 estimated types of dives. They are in the estimated order of prevalence.

For the next analysis, a representation alternate to $\hat{k}_j$ above is useful. Suppose a vector-valued series is constructed whose components are 0-1 valued series corresponding to a particular dive types. In particular set

$$X_{kj} \ = \ 1 \quad if \ \hat{k}_j \ = \ k$$

and $=$ 0 otherwise for $k \ = \ 1, ..., 9$ and $j \ = \ 1, 2, ...$ Then $\mathbf{X}_j$, $j = 1, 2, 3, ...$ is a time series indexed by dive number j.

This vector-valued series may now be examined for serial dependence and for interdependence of components. Figure 4 provides estimates of the power spectra, of the 9 components, obtained by averaging 14 periodograms each based on successive stretches of length 256. The vertical arrows indicate the width of approximate 95 percent marginal confidence intervals. When it appears, the high peak on the left corresponds to the seal's regularly diving about 70 times per day. Interestingly series 7 could be white noise, corresponding to that dive type appearing randomly throughout the migration. The other series appear to be far from white noise. For example, the elevated values on the left could correspond to that particular dive type appearing in clusters.

It is of interest to look into the interdependence of the dive types. Because the data have multinomial character, i.e. some dive type has to occur at each time j, the series cannot be completely independent. To alleviate this dependence only the first 8 components of the series will be retained for the next analysis.

A classic test of multivariate dependence is based on comparing the determinant of a sample covariance matrix to the product of the sample variances. A time series extension of this is given in [33]. The likelihood ratio test statistic considered here, of the hypothesis of independence in the stationary time series case, is given by

$$-2n \ \sum_k (\ \sum_{i=1}^{8} log \ \hat{f}_{ii}(\lambda_k) \ - \ log \ \hat{\mathbf{f}}(\lambda_k) \ ) \tag{7}$$

where λ_k are the frequencies at which the spectral density matrix, $\mathbf{f}(\lambda)$, is estimated and n is the number of periodograms averaged in forming the spectrum estimates.

These computations were carried out with $n \ = \ 28$. Figure 5 provides the individual terms of (7) and the approximate upper 99 per cent marginal null level in the case of independence as a horizontal line. (This last is based on a chi-squared distribution with 8(8-1) = 56 degrees of freedom.) The statistic is above the null level steadily suggesting the presence of some substantial interdependence of the components. The high peak again corresponds to the animal's regularly diving about 70 times per day. The different dive types appear to be particularly tied together at that frequency.

The sampling variability of the $\hat{k}$ has also been ignored in these calculations.

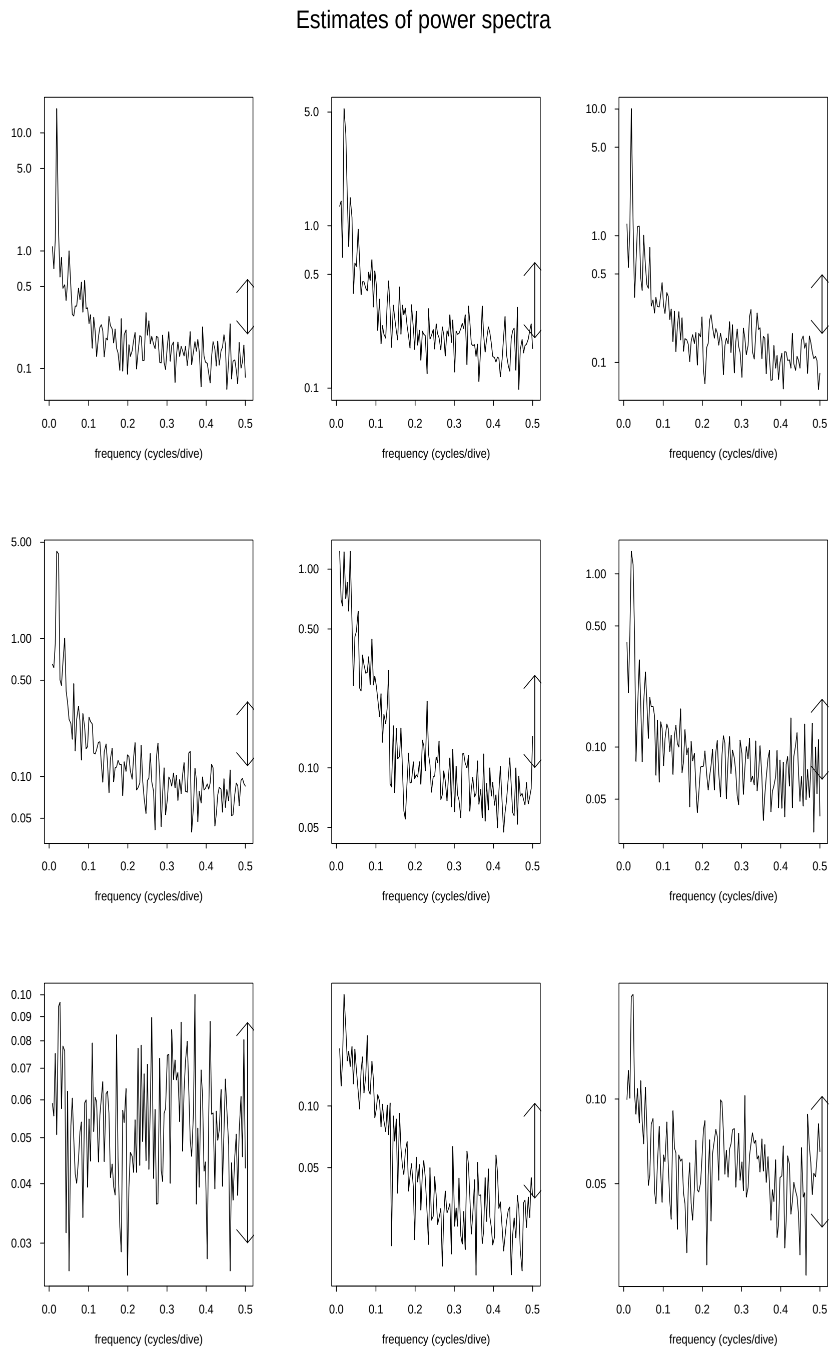

FIGURE 4. Power spectral estimates, for the 0-1 series corresponding to the estimated dive types, obtained by averaging periodograms. The arrows give approximate 95 % confidence bounds.

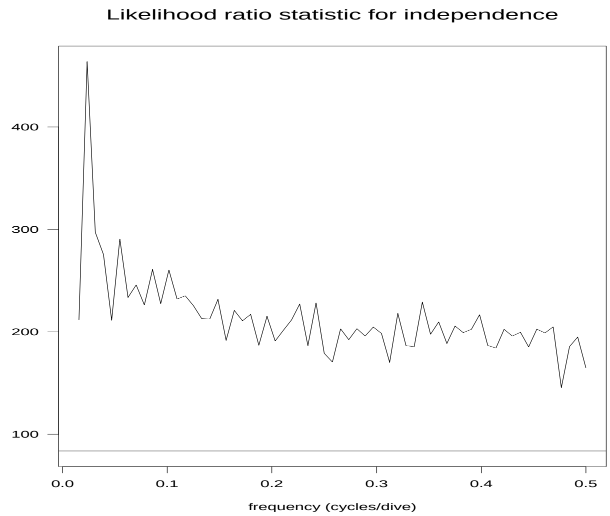

FIGURE 5. Independence test statistic and approximate upper 99 percent null line.

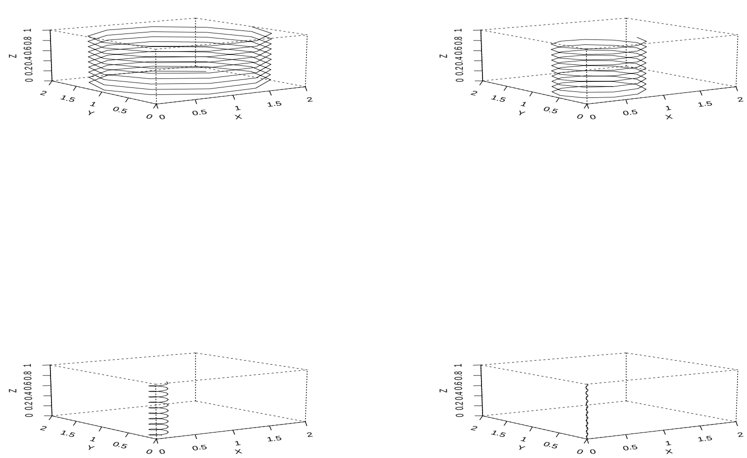

FIGURE 6. Four descents with the same time-depth curve.

Papers concerned with categorical-valued longitudinal data include [21] and [16].

6 Discussion and Summary

There are important difficulties of interpretation of the results of the analyses. Figure 6 shows 4 different possible descent paths of an animal. Each have same time-depth curve, $Y(u) = -\beta u$, yet the paths are very different. The actual descent could in fact be a combination of these. The situation is that conclusions must be drawn carefully. More sophisticated measuring equipment capable of fine scale spatial positioning is required to address this difficulty.

The noise in (2) was taken as statistically independent at the various lags, however it could be modelled as dependent. Then a covariance matrix would be estimated at expression (4) of the EM algorithm.

These preliminary studies indicate that temporal dependence needs to be incorporated into studies of migration to determine whether regularities in behavior imply broad spatio-temporal regularity in the distribution of prey resources or whether oceanographic conditions, season and geographic location influence foraging behavior. Further, additional studies of the spatial components of individual dives are needed to determine how they may confuse or support interpretations of dive form and function based on the necessarily limited shapes that can be categorized from two-dimensional descriptions derived from depth vs. time data series.

7 References

[1] Bengtson, J.L. and Stewart, B.S. (1992). Diving and haulout patterns of crabeater seals in the Weddell Sea, Antartica during March 1986. *Polar Biology* **12,** 635-644.

[2] Brillinger, D. R. (1973). The analysis of time series collected in an experimental design. Pp. 241-256 in *Multivariate Analysis III* Ed. P. R. Krishniah. Academic, New York.

[3] Brillinger, D. R. (1980). Analysis of variance and problems under time series models. Pp. 237-278 in *Handbook of Statistics Vol. 1* Ed. P. R. Krishnaiah. North-Holland, Amsterdam.

[4] Brillinger, D. R. (1981). Some aspects of the analysis of evoked response experiments. Pp. 155-168 in *Statistics and Related Topics* Eds. M. Csorgo, D. A. Dawson, J. N. K. Rao and A. K. Md. E. Saleh. North-Holland, Amsterdam.

[5] Brillinger, D. R. (1997). A particle migrating randomly on a sphere. *J. Theor. Prob.* in press.

[6] Brillinger, D. R. and Stewart, B. S. (1997a). Elephant seal movements: some frequency based studies. *Rev. Bras. Prob. Stat.* in press.

[7] Brillinger, D. R. and Stewart, B. S. (1997b). Elephant seal movements: modelling migration. Submitted.

[8] Brillinger, D. R., Stewart, B. S. and Wong, A. (1995). Computer-assisted, automatic evaluation of two-dimensional profiles (time vs. depth) of time series data for diving marine mammals. Poster at Eleventh Biennial Conference on the Biology of Marine Mammals, Orlando.

[9] Chappell, M. A., Shoemaker, V. H., Janes, D. N., Bucher, T. L., and Maloney, S. K. (1993). Diving behavior during foraging in breeding Adelie penguins. *Ecology* **74,** 1204-1215.

[10] Crocker, D. E. (1994). Swim speed and dive function in a female northern elephant seal. Pp. 328-339 in *Elephant Seals: Population Ecology, Behavior, and Physiology.* Eds. B. J. Le Boeuf and R. M. Laws. University of California Press, Berkeley.

[11] Dempster, A. P., Laird, N. and Rubin, D. H. (1977). Maximum likelihood from incomplete data via the EM algorithm. *J. Roy. Statist. Soc. B* **39,** 1-38.

[12] DeLong, R.L. and Stewart, B.S. (1991). Diving patterns of northern elephant seal bulls. *Marine Mammal Science* **7,** 369-384.

[13] Diggle, P. J., Liang, K-Y. and Zeger, S. L. (1993). *The Analysis of Longitudinal Data.* Oxford Univ. Press, Oxford.

[14] Fahrmeir, L. and Tutz, G. (1994). *Multivariate Statistical Modelling Based on Generalized Linear Models.* Springer-Verlag, New York.

[15] Freeman, W. J. (1980). Measurement of cortical evoked potentials by decomposition of their wave forms. *J. Cybernetics Infor. Sci.* **2,** 44-56.

[16] Gilula, Z. and Haberman, S. J. (1994). Conditional log-linear models for analyzing categorical panel data. *J. Amer. Statist. Assoc.* **89,** 645-656.

[17] Hindell, M. A., Slip, D. J. and Burton, H. R. (1991). The diving behaviour of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia; Phocidae). *Australian J. Zoology* **39,** 595-619.

[18] Jones, M. C. and Rice, J. A. (1992). Displaying the important features of a large collection of similar curves. *American Statistician* **46,** 140-145.

[19] Jones, R. H. (1993). *Longitudinal Data With Serial Correlation.* Chapman and Hall, London.

[20] Jonker, F. C. and Bester, M. N. (1994). The diving behaviour of adult southern elephant seal, *Mirounga leonina*, cows from Marion Island. *South African J. Antarctic Research* **24,** 75-93.

[21] Kalbfleisch, J. D. and Lawless, J. F. (1985). The analysis of panel data under a Markov assumption. *J. Amer. Statist. Assoc.* **80,** 863-871.

[22] Kooyman, G. L., Cherel, Y., Le Maho, Y., Croxall, J. P., Thorson, P. H., Ridoux, V. and Kooyman, C. A. (1992). Diving behavior and energetics during foraging cycles in King Penguins. *Ecological Monographs* **62,** 143-163.

[23] Laird, N. (1978). Nonparametric maximum likelihood estimation of a mixing distribution. *J. Amer. Statist. Assoc.* **73,** 805-811.

[24] Rao, C. R. (1958). Some statistical models for comparison of growth curves. *Biometrics* **14,** 1-17.

[25] Redner, R. A. and Walker, H. F. (1984). Mixture densities, maximum likelihood and the EM algorithm. *SIAM Review* **26,** 195-202.

[26] Schreer, J. F. and Testa, J. W. (1995). Statistical classification of diving behavior. *Marine Mammal Science* **11,** 93-96.

[27] Schreer, J. F. and Testa, J. W. (1996). Classification of Wedell seal diving behavior. *Marine Mammal Science* **12,** 227-250.

[28] Segal, M. R. (1994). Representative curves for longitudinal data via regression trees. *J. Comp. Graph. Stat.* **3,** 214-233.

[29] Stewart, B. S. and DeLong, R. L. (1995). Double migrations of the northern elephant seal. *J. Mammalogy* **76,** 196-205.

[30] Stewart, B. S. and Huber, H. R. (1993). *Morounga angustirostris.* *Mammalian Species* **449,** 1-10.

[31] Stewart, B. S., Leatherwood, S., Yochem, P. K. and Heide-Jorgensen,M. P. (1989). Satellite telemetry of locations and dive durations of a free-ranging harbor seal (*Phoca vitulina richardsi*) in the Southern California Bight. *Marine Mammal Science* **5,** 361-375.

[32] Stewart, B. S., Yochem, P. K., Huber, H. R., DeLong, R. L., Jameson, R. J., Sydeman, W., Allen, S. G. and Le Boeuf, B. J. (1994). History and present Status of the northern elephant seal population. Pp. 29-48 in *Elephant Seals: Population Ecology, Behavior and Physiology* Eds. B. J. Le Boeuf and R. M. Laws. University of California Press, Los Angeles.

[33] Wahba, G. (1968). On the distribution of some statistics useful in the analysis of jointly stationary time series. *Ann. Math. Statist.* **39,** 1849-1862.