



Analyzing temporally correlated dolphin sightings data using generalized estimating equations

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ABSTRACT

Many of the statistical techniques commonly used in ecology assume independence among responses. However, there are many marine mammal survey techniques, such as those involving time series or subgroups, which result in correlations within the data. Generalized estimating equations (GEEs) take such correlations into account and are an extension of generalized linear models. This study demonstrates the application of GEEs by modeling temporal variation in bottlenose dolphin presence from sightings data. Since dolphins could remain in the study area for several hours resulting in temporal autocorrelation, an autoregressive correlation structure was used within the GEE, each cluster representing hours within a day of survey effort. The results of the GEE model showed that there was significant diel, tidal, and interannual variation in the presence of dolphins. Dolphins were most likely to be seen in the early morning and during the summer months. Dolphin presence generally peaked during low tide, but this varied among years. There was a significantly lower probability of dolphins being present in 2003 than 2004, but not between 2004 and the other years (1991, 1992, and 2002). GEE-model fitting packages are now readily available, making this a valuable, versatile tool for marine mammal biologists.

Key words: bottlenose dolphin, correlations, GEE, interannual variation, temporal variation, tidal cycle, *Tursiops truncatus*.

Many studies of marine mammals aim to relate abundance or behavior to the seasonal, diel, and tidal cycles that may influence factors such as habitat or prey availability (Rayment *et al.* 2010, Scott *et al.* 2010), the presence of predators (Heithaus and Dill 2006, Sheppard *et al.* 2009), or variations in human disturbance levels (Lusseau 2005, Thompson *et al.* 2010). However, many of the commonly used statistics in such studies assume independence among responses, which is typically not valid in these temporally autocorrelated data sets (Diggle *et al.* 1994). These data sets can therefore be considered as pseudo-replicated data. One approach is to eliminate values close together (*e.g.*, Mendes *et al.* 2002), so that those remaining can

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be considered independent, but this may remove valuable data and severely reduce the sample size of the data set.

There are two main approaches to modeling clustered data that include correlated responses (Dobson 2002). One approach is based on the hierarchical structure of the study, where correlation is the result of subject-specific effects (Fieberg *et al.* 2009). These may be treated as random effects within a mixed model, where subjects are assumed to be a random sample from a population and variability among subjects reflects heterogeneity due to unmeasured factors. Several random effects may be nested within each other within a multilevel study design (Carlin *et al.* 2001). Random effects models are appropriate when the research focus is on the change in individuals' responses (Fieberg *et al.* 2009). However, this approach assumes random effects covary equally across all observations within a group and are represented by a normally distributed intercept and slope (Dobson 2002). If this is violated and there is consequently a high variance, wide dispersion of the random intercepts and higher parameter estimates may result (Carlin *et al.* 2001). The use of penalized quasi-likelihood within a mixed model (Breslow and Clayton 1993) or Bayesian methods may be more appropriate in these situations (Best *et al.* 1996, Beale *et al.* 2010). Bayesian formulations have the advantage that when the response probabilities are small and the data are highly discrete, information on variance components is contributed by the prior distribution (Breslow and Clayton 1993, Ellison 2004). The freely available software WinBUGS can be used for Bayesian modeling (Lunn *et al.* 2000), but shall not be discussed further here as we shall focus on non-Bayesian methods.

The second approach models the correlation structure explicitly. A repeated measures ANOVA provides a technically simple method and is commonly used in split-plot designs (Diggle *et al.* 1994). However, there are many limitations to the technique as it generally requires balanced and complete data sets, and is restricted to the analysis of normally distributed response variables. Generalized estimating equations (GEEs) provide an alternative approach to overcome these issues (Zeger and Liang 1986). They are most commonly applied when the population-averaged response (marginal mean) is of primary interest and the correlation is considered a nuisance (Zeger and Liang 1986). GEEs do not estimate the distributional properties of the subjects themselves (Zuur *et al.* 2009). The mean response depends only on the covariates and not on the random effects (Fieberg *et al.* 2009, Zuur *et al.* 2009). GEEs have been increasingly used in biomedical analysis (Hutchings *et al.* 2003), social studies (Ballinger 2004), and political studies (Zorn 2001). However, they are only beginning to be used in ecological studies (Lennon *et al.* 2003, Bishop *et al.* 2004, Wilson *et al.* 2005, Panigada *et al.* 2008, Fieberg *et al.* 2009, Koper and Manseau 2009, Villarin *et al.* 2009).

GEEs are an extension of generalized linear models (GLMs) (Liang and Zeger 1986). In a GLM an identity matrix is used to describe the covariance structure, which means that values outside of the main diagonal are fixed at zero, because independence is assumed, whereas in a GEE this is not the case and the matrix off-diagonal elements can be nonzero (Zuur *et al.* 2009). GEEs are highly flexible in terms of the distribution of response variables that can be accommodated, explanatory variables may be continuous or categorical, and missing response values may occur as long as they are missing completely at random (Zeger and Liang 1986). A correlation structure is specified for observations within a group (cluster), but separate clusters are assumed to be independent although they share the same correlation matrix (Liang and Zeger 1986). There are several available correlation structures, but GEEs yield

consistent estimates even with misspecification of the working correlation matrix (Liang and Zeger 1986).

This paper aims to highlight the potential use of GEEs in marine mammal studies that involve correlated data sets. GEE model fitting facilities are available in several general purpose statistical packages including SAS (procedure GENMOD), S-PLUS, and R (Horton and Lipsitz 1999, Zuur *et al.* 2009). Here, we demonstrate its application by analyzing temporal variation in bottlenose dolphin (*Tursiops truncatus*) presence within a narrow coastal channel. Bottlenose dolphin behavior can vary over periods ranging from a tidal cycle (Mendes *et al.* 2002) to a decade (Wilson *et al.* 2004), and in many cases may be influenced by factors operating at multiple temporal scales. It is therefore important to use analytical techniques that can disentangle the interacting effects of environmental variations occurring over these different cycles. Since dolphins can remain within a small study area such as this for several hours (Mendes *et al.* 2002, Hastie *et al.* 2004), sequential hourly observations may be correlated. Here, we demonstrate how statistical analyses using GEEs will take this correlation into account. These results are compared with those from a standard GLM and a generalized linear mixed model (GLMM). In addition, we conducted simulations to investigate the impact of sample and cluster size on the performance of the GEE model.

METHODS

Bottlenose Dolphin Surveys

Observations were made overlooking the Chanonry narrows (57°35'N, 4°06'W), a 1.3-km-wide channel in the inner Moray Firth, Scotland. Dolphin sightings are concentrated in this channel and it is a known foraging ground (Wilson *et al.* 1997, Bailey and Thompson 2006). Differences in dolphin movements and behavior have been identified spatially within this channel (Bailey and Thompson 2010), and here we aimed to identify temporal variations in usage that may further explain the dolphins' foraging strategy.

Dedicated land-based dolphin surveys were conducted by trained volunteers. Data were collected on the same day (Sunday) every week during May 1991 to December 1992 and from July 2002 to December 2004. Due to differences in day-length, winter surveys (October–April) were conducted for 4 h and those in the summer (May–September) for 12 h. The area in view was continually scanned throughout these surveys, and observers recorded the presence of dolphins within a standard area marked by navigation buoys, together with information on group size. Environmental data on sea state, wind direction, and visibility were also collected hourly.

Data Analysis

Thompson *et al.* (2000) found that variability among volunteer observers could be high, but such data could provide a reliable estimate of dolphin presence or absence. Dolphin sightings were therefore coded as present (1) or absent (0) within the study area for each hour of survey effort. Temporal variation in the probability of dolphins being present was examined for tidal, diel, seasonal, and interannual scales.

Tidal state (t) was categorized as hours before or after high water (0). Since tides are periodic phenomena, these tidal states can be described by the angular equivalent of the state of the cycle using sine and cosine functions (Zar 1984, Gibson *et al.* 1996).

Tidal state was therefore converted to two vectors by defining sine (T_S) and cosine (T_C) terms (Fisher 1993):

$$T_S = \sin\left(\frac{2\pi \times t}{12}\right),$$

$$T_C = \cos\left(\frac{2\pi \times t}{12}\right).$$

The cosine term T_C reflects changes from low water to high water and the sine term T_S reflects the differences between the ebb and flood tide (Gibson *et al.* 1996). Seasons and time of day also form part of a cycle. The hour of the day (b), with surveys spanning from 0500 to 1600, was converted to the sine and cosine vectors termed H_S and H_C .

$$H_S = \sin\left(\frac{2\pi \times b}{24}\right),$$

$$H_C = \cos\left(\frac{2\pi \times b}{24}\right).$$

Day of year (d) was similarly converted to vectors termed M_S and M_C .

$$M_S = \sin\left(\frac{2\pi \times d}{365}\right),$$

$$M_C = \cos\left(\frac{2\pi \times d}{365}\right).$$

The denominator of the equations for M_S and M_C was changed to 366 for days in the years 1992 and 2004, which were leap years. Year (Y) was included as a categorical variable as not all of the years were contiguous. The reference level for year was assigned as 2004 because this was the year with greatest survey effort. Sighting conditions can vary based on sea state. Beaufort sea state (S) was therefore included as a continuous variable in the model to account for the probability of sighting dolphins decreasing with increasing Beaufort sea states (Barlow *et al.* 2001, Redfern *et al.* 2008).

Since the response variable (presence/absence of dolphins) was binary and the presence of dolphins within an hour was likely to be affected by whether they were present in the previous hour, a marginal GEE approach was used with a binomial error distribution and logit link function. Examination of the data suggested that the relationship between dolphin presence, time of day, tidal state, and day of year varied among years. We therefore performed the model with interactions with year (Y) included and then repeated this with the interaction terms removed sequentially. We determined which interaction terms should be retained using a Wald test on these models (Zuur *et al.* 2009). This identified that the interactions between year

and tidal state, and with day of year should be included in the final model. The model was defined as the logistic equation:

$$\begin{aligned} \text{logit}(P_{ij}) = & \alpha + \beta_1 H_{Sij} + \beta_2 H_{Cij} + \beta_3 T_{Sij} + \beta_4 T_{Cij} \\ & + \beta_5 M_{Sij} + \beta_6 M_{Cij} + \beta_{7k} Y_{ij} + \beta_8 S_{ij} \\ & + \beta_{9k} Y_{ij} \times T_{Sij} + \beta_{10k} Y_{ij} \times T_{Cij} + \beta_{11k} Y_{ij} \\ & \times M_{Sij} + \beta_{12k} Y_{ij} \times M_{Cij}, \end{aligned}$$

where P_{ij} denotes the probability of dolphins being present in hour i of day j , α represents the intercept, and $\beta_1, \dots, \beta_{12}$ are the coefficients with k indicating the four coefficients for the years 1991, 1992, 2002, and 2003. The logit link function converts the probability to the natural log of the odds. The log of the odds can then be modeled as a linear function of the explanatory variables. The logit link function is

$$\text{logit}(P_{ij}) = \log\left(\frac{P_{ij}}{1 - P_{ij}}\right).$$

The data were ordered chronologically and clusters were defined as days, each of which contained a varying number of consecutive hours of observations.

The identity matrix in the variance function of a GLM assumes independence and this is replaced in a GEE with a correlation matrix (Hardin and Hilbe 2003). Dependence among observations is therefore taken into account in a GEE by specifying the correlation structure, which is then used in the estimate of the covariance matrix (Zeger and Liang 1986). There are several available correlation structures. In this case, an autoregressive correlation structure was implemented, as the association among observations was assumed to be time dependent. This means that the presence of dolphins in an hour affects the probability of them being present in the second hour, but has less affect on the probability for the third hour and so on. The working correlation matrix (\mathbf{R}) for measurements for day i is

$$R_i(\alpha) = \begin{bmatrix} 1 & \alpha & \alpha^2 & \dots & \alpha^{n-1} \\ \alpha & 1 & \alpha & \dots & \alpha^{n-2} \\ \alpha^2 & \alpha & 1 & \dots & \alpha^{n-3} \\ \vdots & & & \ddots & \vdots \\ \alpha^{n-1} & \dots & \alpha & 1 & \end{bmatrix},$$

where α is the intraclass correlation coefficient, $|\alpha| < 1$, and n is the cluster size. In this case, α is the correlation between consecutive survey hours, the cluster size is the number of survey hours in a day (maximum = 12), and the number of clusters is the number of survey days. Separate days were treated as independent as autocorrelation plots of the weekly mean probability of dolphin presence showed only a seasonal series pattern (Venables and Ripley 2002).

The GEE model is fit by first computing an initial estimate of the covariance matrix (\mathbf{V}_i) and the β coefficients using an ordinary GLM, assuming the scale parameter (φ)

is 1 and independence of observations. The covariance matrix is defined as

$$V_i = \phi \times A_i^{\frac{1}{2}} \times R_i(\alpha) \times A_i^{\frac{1}{2}},$$

where A_i is a diagonal matrix containing the variances (Zuur *et al.* 2009). The working correlation matrix and scale parameter are then updated based on these parameters and the covariance matrix is recalculated. The β coefficient estimates are updated and these steps are iterated until there is convergence (Zeger and Liang 1986). At convergence, the regression coefficients are consistent and provide valid standard errors even with misspecification of the correlation structure (Liang and Zeger 1986).

Since GEEs are not based on maximum likelihood, likelihood-ratio tests for model fit cannot be used. The GEE approach currently suffers from a lack of goodness of fit statistics and those that have been proposed are not automatically computed through the major GEE software packages. A Wald–Wolfowitz run test was performed to test whether the residuals were randomly distributed (Chang 2000) and an extension of R^2 for GEEs was calculated (Zheng 2000).

Model Comparisons

The GEE model was compared with a GLM and a GLMM. The GLM assumes independence among observations, whereas the GLMM accounts for correlation in observations through the inclusion of a random effect. Since the response was binary, the GLM model was a logistic regression, which can be considered to be a special case of a GLM. The GLMM was performed with a binomial error distribution, logit link function, and the survey day as a random effect. Comparisons were made between the coefficient and standard error estimates of these models and those from the GEE with the autoregressive correlation structure. The difference in efficiency between the models was also assessed based on the mean square error (MSE) values. The MSE is an optimality criterion that incorporates both bias and variance (Schildcrout and Heagerty 2005). The model with the smallest MSE is generally interpreted as best explaining the variability in the observations.

There are several options for GEE correlation structures, including an independence structure (Hardin and Hilbe 2003). An exchangeable correlation structure assumes within-cluster observations are equally correlated (such as within-subjects) whereas an autoregressive structure is generally used when the correlation is a function of time. An unstructured correlation matrix estimates all possible correlations among within-cluster responses and can be a useful approach if the correlation structure is not known (Zuur *et al.* 2009). However, it requires more parameters to be estimated and can suffer from numeric problems (Hardin and Hilbe 2003). The GEE was repeated with these other correlation structures and the fit of these models compared based on the relative size of the empirical (robust) and model-based (naïve) standard errors. When these standard error estimates are similar, this indicates that the working correlation matrix is more consistent with the observed association (Bishop *et al.* 2000). The correlation structure producing the ratio of empirical to model-based standard error estimates closest to 1 was therefore identified as fitting best (Bishop *et al.* 2000, Koper and Manseau 2009). It is the empirical standard errors, which are robust to misspecification of the correlation structure, that are generally used for determining statistical significance (Koper and Manseau 2009).

Simulations

In our study, there was less survey effort during the winter months and cluster size (the number of survey hours per day) therefore varied. Simulations were conducted to determine the effect of sample size, cluster size, and number of cluster replicates on the performance of the GEE model. The data for these simulations were generated using the original data set so the complexity of the data set was retained. In order to generate a simulated data set that possessed a similar correlation structure as the observed binary sightings data we used the approach of Emrich and Piedmonte (1991). This was achieved by using the working correlation matrix and fitted values from the GEE autoregressive model to generate Bernoulli variates, which produced correlated binary outcomes for the simulated response (Emrich and Piedmonte 1991). First we created a data set of the same length as the observed data by using the fitted values from the GEE autoregressive model (\hat{p}_j). Then we generated a multivariate normal data set, $\mathbf{Z} = (Z_1, \dots, Z_j)'$, with zero mean and a correlation matrix based on the working correlation matrix from the GEE model. The resulting correlation matrix was occasionally not positive semidefinite (which requires a matrix multiplied by a vector to be greater than or equal to zero) and in these cases we used the `make.positive.definite` function in the R software `corpcor` package (Schaefer *et al.* 2009) to find a similar positive definite one. Finally, for $j = 1, \dots, J$, where J is the length of the data set, the response (Y_j) is set to 1 if $Z_j \leq z(\hat{p}_j)$, otherwise $Y_j = 0$, where z is the normal quantile function. The simulation was repeated for 1,000 iterations and the number of iterations for H_S with Z -values < -1.96 or $> +1.96$ counted and compared to the expected value of 5% based on a normal distribution. The effect of sample size on model performance was investigated for the GLM and GEE models by performing simulations with data from a quarter ($n = 392$), half ($n = 784$), and three-quarters ($n = 1,176$) of the original data set ($n = 1,569$). At these sample sizes, uniform clusters of size 4, 8, or 12 (relating to different survey day lengths) were created to investigate the impact of varying the number and size of clusters on the GEE model.

We also investigated the minimum effect size that could be detected as statistically significant by varying the level of an imposed diel effect. The simulated data sets were generated by retaining the explanatory variable values from the original data set and only changing the response values. The response variable was generated by randomly selecting from two uniform continuous distributions. The uniform continuous distribution was set for values between 0 and 1 after 1100, but the minimum value was increased from 0 in 0.02 increments for times before 1100. This thereby gradually raised the mean probability of dolphins being present for the earlier hours. For each increment in the mean probability, 1,000 simulated data sets were created. The probability values were converted to a dichotomous variable by assigning values > 0.4 as 1 and those ≤ 0.4 as 0, where 0.4 was the mean sighting probability of the original data set. The GEE model was applied to each simulated data set. We did not simulate a specific correlation structure so that the results would be more widely applicable, and therefore applied the unstructured correlation matrix in the GEE. The minimum effect that could be detected was determined by the smallest rise in probability that resulted in the time of day, H_S , explanatory variable being given as statistically significant in the GEE model in at least 95% of the iterations. Any changes to the statistical significance of other explanatory variables, for which no effect on the response variable had been imposed, were also noted. All statistical analyses were performed using the software R version 2.8.0

Table 1. Results from the generalized estimating equation (GEE) model with autoregressive correlation structure. Variables with $P < 0.05$ are indicated by an asterisk. Year was specified as a categorical variable where the reference level was 2004.

Parameter	Coefficient estimate	Standard error	Wald	P
Intercept	-0.781	0.336	5.400	0.020*
Time				
H_S	0.362	0.126	8.257	0.004*
H_C	0.061	0.247	0.061	0.805
Tide				
T_S	-0.168	0.212	0.632	0.427
T_C	0.039	0.211	0.034	0.855
Day of year				
M_S	0.598	0.210	8.078	0.004*
M_C	-1.773	0.321	30.509	< 0.001*
Year				
1991	0.158	0.345	0.210	0.646
1992	0.415	0.268	2.401	0.121
2002	0.969	1.106	0.768	0.381
2003	-1.179	0.360	10.752	0.001*
Sea state	0.018	0.059	0.098	0.754
Interactions				
T_S : Year 1991	-0.232	0.322	0.520	0.471
T_S : Year 1992	0.088	0.292	0.090	0.764
T_S : Year 2002	0.069	0.471	0.022	0.883
T_S : Year 2003	-0.586	0.283	4.305	0.038*
T_C : Year 1991	-0.389	0.286	1.858	0.173
T_C : Year 1992	-0.518	0.268	3.717	0.054
T_C : Year 2002	-0.277	0.272	1.037	0.309
T_C : Year 2003	-0.019	0.264	0.005	0.943
M_S : Year 1991	-0.351	0.364	0.930	0.335
M_S : Year 1992	-0.577	0.294	3.858	0.049*
M_S : Year 2002	1.895	1.401	1.830	0.176
M_S : Year 2003	-0.473	0.396	1.429	0.232
M_C : Year 1991	0.474	0.472	1.010	0.315
M_C : Year 1992	1.264	0.404	9.802	0.002*
M_C : Year 2002	-0.773	0.643	1.444	0.230
M_C : Year 2003	-0.087	0.483	0.033	0.857

(R Development Core Team 2008), and the contributed packages *geepack* version 1.0–17 (Yan and Fine 2004), *gee* version 4.13–13 (Carey *et al.* 2007), *corpcor* version 1.5.2 (Schaefer *et al.* 2009), and *arm* version 1.2–8 (Gelman *et al.* 2009).

RESULTS

Temporal Variation in Bottlenose Dolphin Presence

There were 1,569 h of survey effort on 199 separate days (number of clusters) with up to 12 survey hours within a day (the maximum cluster size). The results of the GEE indicated that there was significant temporal variation in the presence of dolphins at a range of scales (Table 1, Fig. 1). In the GEE autoregressive model, a significant

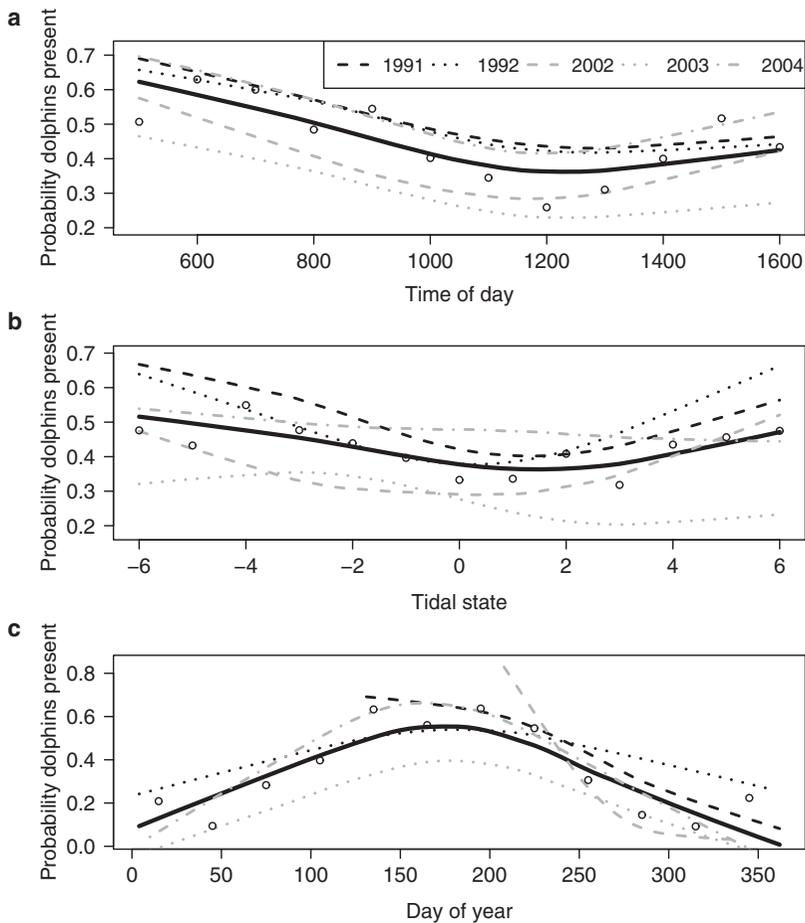


Figure 1. Best-fit lines for the fitted values from the generalized estimating equation (GEE) autoregressive model of the probability of dolphins being present for: (a) time of day (GMT), (b) tidal state, hours before and after high water (0), (c) day of year. The solid black line shows the mean, the dashed lines in black are the years 1991 and 1992, and those in gray the later years 2002, 2003, and 2004. The mean proportion of survey hours in which dolphins were present are shown as circles (calculated as a monthly mean for day of year).

relationship was detected between the probability of dolphins being present and the time of day (H_S , $P = 0.004$; Table 1). The probability was highest between 0500 and 0800, declined until 1200, and then rose again during the afternoon (Fig. 1a). There was also a significant relationship with the tidal cycle, which varied among years (Table 1). The probability that dolphins were present was generally lowest at high water (0) to 2 h afterwards (+2), and highest at low water (-6 and +6) (Fig. 1b). However, the relationship was significantly different in 2003 than in 2004 (T_S : Year 2003, $P = 0.038$). In 2003, the highest probability of presence occurred 2–4 h before high water (a flood tide) and then dropped to its lowest value at 2–4 h after high water (an ebb tide) (Fig. 1b).

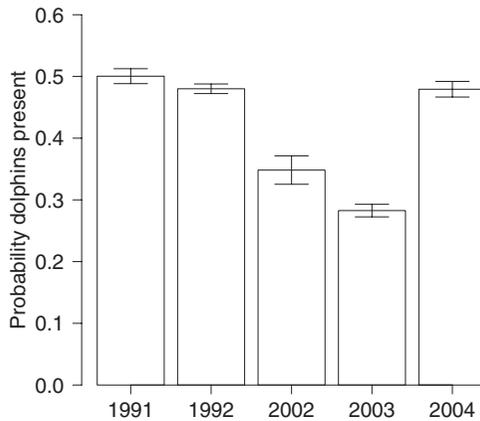


Figure 2. The mean (and SE) probability of dolphins being present from the fitted values of the GEE autoregressive model in relation to year. Note years are not all successive.

There was a significant seasonal cycle in the probability of dolphins being present (Table 1). The probability peaked during the middle of the year (summer months) and was lowest at the start and end of the year during the winter (Fig. 1c). The relationship was significantly different in 1992 than in 2004 (M_S : Year 1992, $P = 0.049$; M_C : Year 1992, $P = 0.002$). The peak in probability of dolphin presence occurred later in the year in 1992 and values were higher in the winter months than in 2004 (Fig. 1c).

There were significant interannual differences in the probability of dolphins being present, with lower odds in 2003 than in 2004 (Odds ratio = 0.307, 95% CI = 0.152–0.622, $P = 0.001$). There was no significant difference in the probability between 2004 and the other years (Table 1, Fig. 2). There was a relatively low mean probability of dolphins being present in 2002 (Fig. 2), but there was also high variability with very high probabilities occurring during the summer and very low at the end of the year in the winter (Fig. 1c). The relationship with sea state was not significant (Table 1), but it still acted as a correction term. The near-zero coefficient estimate for sea state (Table 1, Fig. 3) provides support that our presence/absence response was robust to different sighting conditions.

The correlation coefficient α from the GEE autoregressive model was 0.258 for consecutive survey hours (Table 2). The estimated scale (dispersion) parameter for the GEE model was 1.003 (Table 2) indicating there was little dispersion, and based on a Wald–Wolfowitz run test we did not reject the null hypothesis that the residuals were randomly distributed ($Z = -0.135$, $P = 0.554$) suggesting the model structure was appropriate. The R^2 value for this model was 0.220, which is comparable with the values in the example by Zheng (2000).

Model Comparisons

The GEE, GLM, and GLMM produced similar coefficient estimates, although they were generally closer to zero in the GEE model (Fig. 3). The logistic regression GLM tended to give the smallest standard errors of the three models and hence identified more of the parameters as statistically significant. The GEE autoregressive model

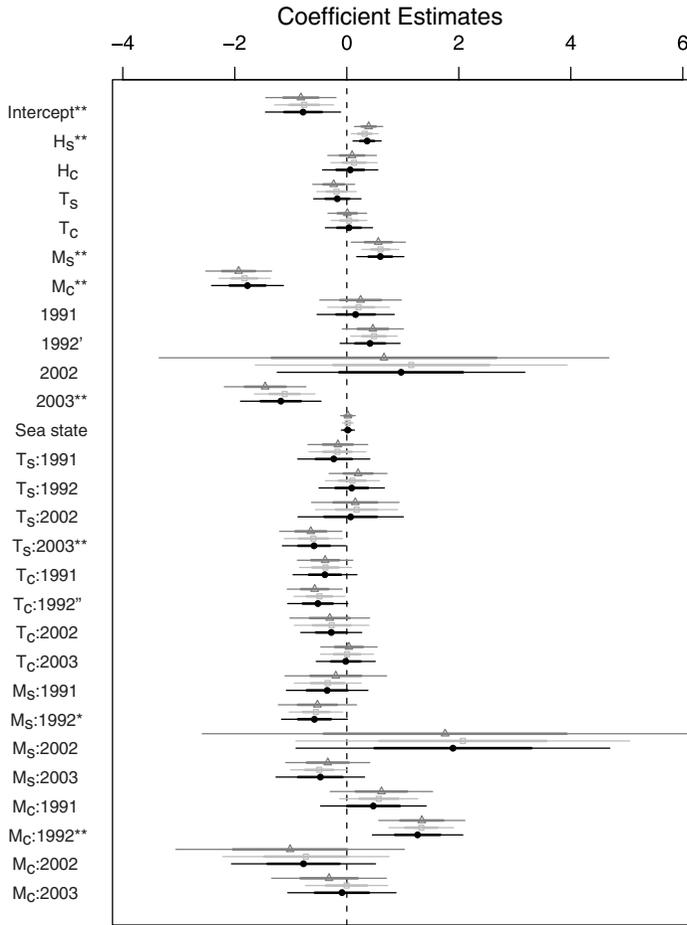


Figure 3. Coefficient estimates for the GEE autoregressive model (black circles), logistic regression (GLM, light gray squares), and generalized linear mixed model (GLMM, dark gray triangles). The thick lines represent the standard error and the thin lines the 95% confidence interval. The symbols indicate whether the coefficient term was significant ($P < 0.05$), where ** denotes it was significant in all three models, * in the GEE and GLM models only, ' in the GLM only, and '' in the GLM and GLMM only.

had a much lower MSE value (0.194) than the GLM (6.407) and GLMM (0.829) indicating greater efficiency.

The GEE model was relatively insensitive to the specified correlation structure. The GEE model with the independence correlation structure had the highest mean ratio of empirical to model-based standard errors at 1.201 (Table 2). A high ratio indicates that the correlation structure did not describe all of the correlation in the data (Koper and Manseau 2009). The autoregressive correlation structure produced a ratio closest to 1 at a value of 0.990 confirming that this was the most sensible choice in terms of the data being time ordered. The unstructured correlation structure

Table 2. Ratio of empirical (robust) to model-based (naïve) standard errors, the correlation (α) between consecutive survey hours, and the scale parameter (φ) from the GEE models with different working correlation structures.

	Independence	Autoregressive	Exchangeable	Unstructured
Intercept	1.278	1.080	1.147	1.071
Time				
H_S	1.069	0.894	1.102	0.973
H_C	1.198	1.043	1.251	1.070
Tide				
T_S	1.156	1.011	1.232	1.085
T_C	1.335	1.096	1.351	1.186
Day of year				
M_S	1.265	1.028	0.963	1.021
M_C	1.390	1.129	1.149	1.119
Year				
1991	1.266	1.009	1.048	1.024
1992	1.279	1.048	1.062	1.038
2002	0.779	0.655	0.611	0.614
2003	1.314	1.073	1.064	1.033
Sea state	1.220	0.998	0.969	1.001
Interactions				
T_S : Year 1991	1.223	1.062	1.283	1.098
T_S : Year 1992	1.210	1.018	1.282	1.103
T_S : Year 2002	1.356	1.087	1.397	1.232
T_S : Year 2003	1.098	0.909	1.130	0.959
T_C : Year 1991	1.230	1.015	1.251	1.086
T_C : Year 1992	1.193	0.988	1.198	1.045
T_C : Year 2002	0.809	0.677	0.824	0.748
T_C : Year 2003	1.122	0.927	1.149	0.988
M_S : Year 1991	1.237	0.970	0.922	1.002
M_S : Year 1992	1.208	0.989	0.938	0.968
M_S : Year 2002	0.933	0.769	0.714	0.738
M_S : Year 2003	1.534	1.244	1.179	1.198
M_C : Year 1991	1.356	1.087	1.111	1.096
M_C : Year 1992	1.381	1.130	1.136	1.103
M_C : Year 2002	0.866	0.717	0.684	0.706
M_C : Year 2003	1.314	1.058	1.030	1.030
Mean ratio	1.201	0.990	1.078	1.012
α	0	0.258	0.098	-0.075-0.329
φ	1.008	1.003	0.999	1.033

produced the next closest value to 1. However, this structure took longer to compute because more parameters are estimated (Hardin and Hilbe 2003).

Simulations

Using the explanatory variables from the original data set with a randomly generated response variable, the number of iterations giving Z-values < -1.96 and $> +1.96$ was close to the expected 5% of iterations for the GEE model, but was

Table 3. Percentage of simulation iterations for which the time of day term H_S had Z-values < -1.96 and $> +1.96$ for a model with random responses for sample sizes equal to the original data set ($n = 1,569$), three-quarters ($n = 1,176$), half ($n = 784$), and a quarter of the sample size ($n = 392$) for the GLM and GEE models. A value of 5% of the iterations was expected based on a normal distribution. "Original data structure" represents where the explanatory variable values have been used in the same order as the original data set and only the response values have been changed. The percentage is also given for the GEE model applied to the simulated data with uniform clusters of size 4, 8, and 12.

Sample size	Original data structure		Uniform cluster size		
	GLM	GEE	4	8	12
1,569	6.60	6.00	4.90	5.50	6.10
1,176	6.90	6.29	5.30	5.65	6.39
784	7.20	6.55	5.87	6.40	6.70
392	8.00	6.80	6.10	6.75	6.95

higher for the GLM (Table 3). The percentage increased with smaller sample sizes and larger cluster sizes (Table 3). At all sample sizes examined, the percentage of Z-values < -1.96 and $> +1.96$ was lowest for the uniform cluster size 4 (the smallest cluster size) indicating that results from the GEE model were most reliable for large numbers of replicates of small clusters.

The minimum effect size that could be detected as statistically significant in at least 95% of iterations was a 0.1 mean increase in the probability of dolphins being present. None of the other explanatory variables, for which no effect had been imposed, were significant.

DISCUSSION

In many field studies of this kind, the degree of correlation among responses is not known. As a result, temporal autocorrelation has often been ignored or observations have been removed to satisfy the assumption of independence. GEEs use within-cluster correlations to increase the efficiency of estimation and allow maximum use of sequential or repeated measures information. Our study demonstrates that when there are correlations among responses, accounting for this within a GEE results in more accurate inferences, and both the coefficient and standard error estimation are improved.

When the number of responses is large, the estimated regression coefficients from the standard GLM should be very similar to that of a GEE model, but the standard errors will be biased (Hu *et al.* 1998). Underestimating the standard errors in the GLM resulted in more of the variables being identified as significant (Fig. 3). The percentage of simulation iterations that were significant was much greater than the expected 5% for the GLM (Table 3). In addition, the GLM percentages departed to a greater degree from 5% for the smaller sample sizes, indicating that the GLM was more sensitive to sample size than the GEE. This provides support for the use of the GEE model, which gave a more accurate accounting of uncertainty in the coefficient estimates. The GEE also had the smallest MSE indicating this model best explained the variability in the observations. This supports the approach used by Panigada

et al. (2008) in which they applied a GEE to account for temporal autocorrelation and produce reliable model standard errors and *P*-values for habitat preferences of fin whales and striped dolphins.

Improvements in statistical efficiency of a GEE over independence models will be greatest when the variance function, cluster, and correlation structure are modeled correctly (Bishop *et al.* 2000). Only correlations within a single cluster stratum can be accommodated by a GEE. Consequently, only correlations between consecutive hours could be included in our study, although weaker correlations between consecutive weeks may also have existed.

Seasonal variation in environmental conditions and other logistic constraints can often lead to unbalanced or missing data and GEEs remain robust as long as the data are missing at random (Zeger and Liang 1986). For example, as a result of variation in daylight, our visual surveys could not be conducted throughout a 12 h period during both winter and summer. This resulted in differences in cluster sizes associated with explanatory variables in the model. Simulations showed that despite confounding effects of diel and seasonal patterns of effort, temporal effects were detected by the model and no falsely significant variables were generated. The GEE was sensitive to even relatively small effects (*i.e.*, 0.1 increase in probability of dolphins being present) of the covariates on the response variable. The robustness of this approach could prove particularly useful in marine mammal research where observational studies are common and data sets are often temporally autocorrelated.

Simulations highlighted that the GEE model performed best with many replicate clusters and Type I errors (rejection of null hypothesis when it is true) were lowest for the smallest cluster size of 4. For a cluster size of 4, Ziegler *et al.* (1998) suggest using GEEs where the number of clusters is greater than 30. However, our simulation results indicate that to maintain a Type I error of close to 5% it is preferable to have an even greater number of clusters. In contrast, many study sites used for marine mammal research are difficult to access, resulting in the tendency to maximize time on the site (which extends cluster size) and minimize the number of visits (which reduces the number of clusters). It can be difficult to balance these factors within logistic and financial constraints, but these simulations point to the benefits of maximizing the number of days on which samples are collected.

Our study indicated that variation in the probability of dolphin presence in this study area occurred at a range of temporal scales. Such variations are likely to reflect the animals' habitat preference (Boyd 1996). Given that there is no evidence of predation (Wilson *et al.* 2004) or specific calving grounds (Grellier 2000) for this population of bottlenose dolphins, temporal variability in habitat selection is likely to result either from changes in prey availability, or some other measure of habitat quality.

At a fine scale, there are associated changes in light, temperature, and water currents over the diel and tidal cycles. These may affect the availability of prey in different areas (Baumgartner *et al.* 2003). Allen *et al.* (2001) observed that feeding in bottlenose dolphins off Clearwater Harbor in Florida peaked at dawn and decreased throughout the day. We discovered an early peak, but also one later in the day. This may be caused by a greater requirement for energy intake at these times or as a result of variations in prey availability or accessibility at different times of the day (Stevick *et al.* 2002). Seal abundance near a channel constriction was also greater during flooding tides and, during this period, the seals caught more large fish (Zamon 2001). Foraging success may similarly be higher within our study area channel explaining the higher probability of dolphin presence during a low and flooding tide. Mendes *et al.* (2002) found that dolphin abundance increased in another narrow

channel in the Moray Firth during the flood tide. They hypothesized that frontal regions increase the accumulation of prey and therefore dolphin foraging efficiency is increased and metabolic costs reduced. Seasonal changes in the movement of dolphins may occur in response to specific prey species preferences and social structure (Wilson *et al.* 1997, Lusseau *et al.* 2006). Our summer peak in the probability of dolphin presence coincides with return of salmonids to their natal rivers (Stewart *et al.* 2009). Bottlenose dolphins in Scottish waters are known to prey on these species (Janik 2000, Santos *et al.* 2001) and have been observed surfacing with salmon in their mouths in this particular channel (Bailey and Thompson 2006). Dolphins in another coastal channel in the Moray Firth were also seen to show a clear seasonal pattern in area use, with a July peak (Hastie *et al.* 2003).

During the 1990s, photo-identification studies revealed that this population expanded its range, most likely in response to changes in prey resources (Wilson *et al.* 2004). Our study found that the occurrence of dolphins in this core part of the population's range showed significant interannual variation. However, the greatest change occurred between the years 2003 and 2004 rather than between the two time periods 1991–1992 and 2002–2004. This is a highly mobile species and may be capable of responding rapidly to seasonal and annual changes in prey. Similar seasonal patterns have been shown for bottlenose dolphins in a number of other areas, likely as a consequence of variability in local conditions causing areas to become more important for foraging (Irvine *et al.* 1981, Miller and Baltz 2010), mating (Wells *et al.* 1980, Urian *et al.* 1996), calving (Scott *et al.* 1990, Haase and Schneider 2001), or avoiding predators (Wells *et al.* 1980, Heithaus and Dill 2002).

Understanding the factors that drive such temporal patterns in occurrence remains a key challenge for many marine mammal research programs. These results highlight that GEEs provide a valuable statistical tool that is robust to the lack of independence in many of the data sets that could provide insights into this question.

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