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Investigations into the relationship between pelagic fish and dolphin distributions off the west coast of Scotland

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Surveys of the main commercially exploited fish stocks are carried out on a regular basis in European waters, and provide promising platforms from which to conduct passive acoustic surveys for cetaceans. This study examines observations of cetacean distribution in relation to simultaneously collected pelagic fish distribution data. A two-element audio (100 Hz – 24 kHz) hydrophone was towed 400m behind a chartered pelagic fishing vessel, Enterprise, during one of the Fisheries Research Services (FRS) annual acoustic surveys for herring (*Clupea harengus*) in July 2004. The survey covered the continental shelf waters (to the 400m depth contour) to the west of Scotland from 56°N to 60°N. 30-second listening stations were carried out every 15 minutes, and dolphin whistle and click sound levels were assessed and noted to provide data on dolphin distribution. A Simrad EK500 echosounder operating at 38, 120 and 200 kHz was used, in conjunction with pelagic trawling, to collect data on the distribution and abundance of herring. The relationship between dolphin and pelagic fish distributions was examined within a multinomial logit model (MLM) framework. Issues associated with such methods have also been discussed, including the difficulty in determining dolphin species from their vocalisations, bias due to changes in vocalisation behaviour, and bias due to diurnal changes in herring behaviour.

Keywords: cetaceans, pelagic fisheries, acoustics, surveys, distribution

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Introduction

The relationship between cetacean and their prey is a critical ecological factor affecting, among other things, their distribution and relative abundance. Only a few studies have directly studied the relationship between cetaceans and their prey (Wishner *et al.* 1995, Fiedler *et al.* 1998, Lindstrom *et al.* 2002, Macleod *et al.* 2004, Croll *et al.* 2005). More commonly, studies of cetacean distributions have investigated habitat preferences in terms of topographical and environmental variables (e.g. Jaquet and Whitehead 1996, Woodley and Gaskin 1996, Baumgartner 1997, Davis *et al.* 1998, Canadas *et al.* 2002, Hastie *et al.* 2005, Macleod *et al.* 2005), which may be considered proxies for prey distribution. Most cetacean-prey studies either examined the distribution of whales with published fisheries data (Macleod *et al.* 2004), or directly with hydroacoustic fish survey data collected within the same year of the cetacean survey data (Lindstrom *et al.* 2002), or carried out focussed hydroacoustic surveys of zooplankton in the vicinity of known baleen whales feeding grounds (Wishner *et al.* 1995, Cotte and Simard 2005, Croll *et al.* 2005). Fiedler *et al.* (1998) conducted one of the only concurrent hydroacoustic and dolphin visual surveys, relating dolphin distribution to acoustic backscatter (as an indicator of prey density). This study found an overall correlation of dolphins with backscatter strength, but carried out no spatial analysis of correlation between the two variables. The paucity of research conducted in this

area of ecology is in part due to the difficulty in conducting simultaneous measurement of predators and their prey, in addition to the large amount of resources required to conduct such surveys.

More recently, passive acoustic methods have become established as a reliable method of surveying for cetacean species (Leaper *et al.* 1992, Clark and Fristrup 1997, Gillespie 1997, Goold 1998, Gordon *et al.* 2000, Hastie *et al.* 2003 & 2005). This method is more automated so requires less people, allowing detection of cetaceans both in poor sea conditions, and during low light levels. These methods also typically have a greater detection range than visual survey methods (Gordon *et al.* 2000). Platforms of opportunity can provide a cost effective means of collecting cetacean data, for example Hastie *et al.* (2005) carried out acoustic surveys for dolphins during oceanographic surveys to the north-west of Scotland, and was able to relate dolphin distributions to environmental variables measured directly during the survey. Hydroacoustic surveys for fish also provide an ideal opportunity to study cetacean distribution in relation to potential prey species. The hydrophone can be towed behind the vessel without interfering with the main objectives of the survey, and brought in quickly prior to trawling.

The abundance and distribution of pelagic schooling fish are regularly determined using active “fisheries” acoustic techniques (Simmonds and MacLennan 2005). This is especially true for abundant pelagic species such as herring (*Clupea harengus*). In summer, herring form large schools in midwater that can be detected effectively by echosounders, providing information that is vital to herring stock assessments (Simmonds 2003). As a means to estimate abundance, acoustic surveys are an efficient tool as they offer almost continuous detection of objects (echotraces) in the whole water column, at a very high resolution (typically 20 cm in the vertical), over large distances. The ICES International North Sea Herring Acoustic Survey (INSHAS) is one such example of a multi-vessel acoustic survey with a time series of over 20 years: see Bailey *et al.* (1998) for a review. The survey takes place each year with the participation of the United Kingdom (Scotland), the Netherlands, Norway, Germany, and Denmark, covering the whole of the North Sea and the west coast of Scotland (ICES 2004). The survey on the west coast of Scotland provides an ideal opportunity to combine passive and active acoustics for dolphins and herring respectively.

The main aim of this study was to investigate the relationship between distributions of dolphins and herring, and to explore one method of evaluating this relationship on a spatial and temporal scale. It was also important to evaluate the amount of spatial and temporal correlation in the datasets, and to relate any patterns in distribution to environmental variables, in order to build environmental models to describe the distributions of herring and dolphins in the area.

Material and methods

The survey was carried out on the chartered Motorised Fishing Vessel (MFV) *Enterprise* in July 2004. The area covered was north and west of Scotland from longitude 4° West to the shelf edge (200 m), as far south as latitude 56° North and as far north as 60° North (Figure 1). The survey design (Figure 1) was stratified according to the expected herring distribution based on results from the survey time series. Regular parallel transects were used along lines of latitude. The transect spacing was set to 15, 7.5 or 3.75 nmi, giving 2, 4 or 8 transects per ICES statistical rectangle respectively. Transect length was variable to extend from close inshore to the shelf edge (400 m). The sea area between the Hebrides and the mainland (the

Minch) is difficult to survey with the above design, so a zig-zag design with 15 n.mi. spacing was adopted. The total cruise track length was 2600 n.mi. (4815 km).

Dolphin data collection

The stereo hydrophone was built according to the IFAW hydrophone design (Gillespie 1997), using two Benthos AQ4 elements mounted close to an HP/01 (Magrec, Devon, UK) low noise individual amplifiers mounted providing a gain of around 30dB. The response of the hydrophone/preamplifier unit is flat within 3dB between 100 Hz and 35 kHz. Hydrophone elements were mounted 3 m apart and sealed within a 35 mm diameter oil-filled polyurethane tube.

The hydrophone was towed 400 m behind the vessel on a kevlar-strengthened towing cable. It was towed throughout the survey, and retrieved & stored on one of the net drums on the middle deck during each trawl. At the ship survey speed of 10 knots, the hydrophone array is likely to sit at a depth of around 6-10m (Gillespie 1997). The hydrophone was connected to the audio amplifier, sound card and computer via a 20 m deck cable.

The hydrophone signal is first passed through an HP27ST amplifier/conditioner unit (Magrec, Devon, UK) where it could be amplified (10-40 dB) and filtered by applying high pass filters at between 100-3600 Hz to filter out low frequency boat noise before passing through a USB Quattro soundcard (M-Audio) sampling at 48k Hz (i.e. giving a maximum frequency of 24 kHz). Data storage is carried out on a laptop running the IFAW logging software package *Logger 2000* (Gillespie 1997), from which 30-second recordings of the hydrophone were made to hard disk every 2 minutes and automatically linked to the GPS location within an Access database. Since it was not possible to listen continuously for the 20-hour survey days with one person, continuous listening was only carried out for half the time. Subsequent to the trip, acoustic listening stations of 30 seconds every 15 minutes were analysed for boat noise (individually for noise originating from the *Enterprise* and for noise from other ships), dolphin whistles and clicks on an arbitrary scale of 0 (inaudible) to 5 (loud). Visual surveys were carried out on an opportunistic basis to try to match species to acoustic vocalisations.

Herring data collection

The methods used to carry out the acoustic survey were common to those employed throughout the INSHAS: these are detailed in the Manual for Herring Acoustic Surveys in ICES Divisions III, IV and VIa (ICES 2004) and follow the general principles described in Simmonds *et al.* (1992) and Simmonds and MacLennan (2005). Acoustic data were collected using a Simrad EK500 scientific echosounder (Bodholt *et al.* 1989), operating three transducers at frequencies of 38, 120 and 200 kHz. The transducers were mounted in a towed body and deployed from the ships crane approximately 3 m off the starboard side amidships at a depth of approximately 3-5 m. The echosounder was configured to ping at each frequency simultaneously, every 1 second, with pulse lengths of 1.0 ms for each frequency. The performance of the echosounders was monitored using standard target calibration techniques (Fernandes and Simmonds 1996). Two good calibrations were carried out at the beginning and in the middle of the survey. The acoustic data were only collected from 03:00 to 23:00 hrs: outwith this collection period (at night) the herring disperse and rise to the surface making them unavailable to the acoustic apparatus.

Major echotrace concentrations were sampled with a pelagic trawl with a net of 20 mm mesh in the codend. When trawling at a speed of approximately four knots the trawl's vertical opening was 12 metres and the horizontal opening was 20 m. A total of 42 trawl catches provided the critical information to identify the echotraces and determine the size and age structure of the population.

Data were logged from the echosounder to a personal computer with SonarData's Echolog software (SonarData Pty Ltd., GPO Box 1387 Hobart, Tasmania, Australia). The raw data were collected as echogram (Q) telegrams consisting of time stamped digitised volume backscattering strengths (VBS). Each pixel on the echogram, therefore, corresponds to a VBS (symbol, S_v ; unit, dB re 1m^{-1}). Other telegrams collected include detected seabed depth and geographic location (latitude and longitude). Data were integrated over 2.5 n.mi. (15 minutes at 10 knots) equivalent distance sampling units (EDSU) to determine the Nautical Area Scattering Coefficient (NASC) for herring. The NASC is proportional to herring abundance (MacLennan *et al.* 2002) and is ultimately used in conjunction with the information from the trawl to determine the abundance of herring at age. For the purposes of the current exercise, the NASC value was summarised into a simple measure of presence/absence within an EDSU.

Data analysis - Autocorrelation

Autocorrelation can exist in a dataset both spatially and temporally. In this study spatial correlation was examined using the variogram – a standard geostatistics tool used in evaluating the spatial structure of fish (Rivoirard *et al.* 2000) and other ecological variables (Bellehumeur *et al.* 1997). The variogram examines the correlation over distance, so for species that move little in time relative to the ships speed (such as herring – Hafsteinsson and Misund 1994). It measures, on average, the half variability between two points, as a function of their distance (Matheron 1971, Rivoirard *et al.* 2000):

$$\gamma^*(h) = 0.5 \frac{1}{N(h)} \sum [I(x_i) - I(x_i + h)]^2$$

where $\gamma^*(h)$ is the experimental variogram, $N(h)$ is the number of pairs of points separated by the distance h , and $z(x)$ is the value of the variable at location x such that:

$$I(x_i) = \begin{cases} 1, z(x) > 0 \\ 0, z(x) = 0 \end{cases}$$

$$I(x_i + h) = \begin{cases} 1, z(x + h) > 0 \\ 0, z(x + h) = 0 \end{cases}$$

For patchy data the variogram levels off at the 'sill', this occurs at a distance called the 'range' (Bellehumeur *et al.* 1997, Rivoirard *et al.* 2000), which is equivalent to the patch diameter of the variable.

For species that are more mobile, such as dolphins, the variogram is likely to have less meaning as the animals are more likely to have moved between the time delay between transects. In this case measuring temporal correlation is probably more meaningful. The autocorrelation function in R (Gilbert & Plumber) was used to calculate the temporal correlation between samples.

Data analysis - Modelling

The relationship between herring and dolphins was examined within a Multinomial Logit Model (MLM) framework, which has previously been used to investigate the interspecific associations between fish species (Beare *et al.* 2003). This model is able to examine the relationship between patchy distributions where there are a high number of zeros in both data sets. If dolphins are taken to be species A, and herring species B, four categories can be defined (with the probability of each category shown in brackets):

1. Absence of both species A and species B (P_{00})

2. Presence of species A and absence of species B (P_{A0})
3. Absence of species A and presence of species B (P_{B0})
4. Presence of both species A and species B (P_{AB})

These probabilities were taken from the multinomial distribution for the four probabilities:

$$P_{00}^{n_0} P_{A0}^{n_1} P_{B0}^{n_2} P_{AB}^{n_3}$$

where n_i is the number of samples in each category i . Beare *et al.* (2003) model the multinomial distribution by rewriting the equation in terms of nested conditional events:

$$\prod_{i=0}^3 p_i^{n_i} (1 - p_i)^{n_0 + \dots + n_{i-1}}$$

with:

$$p_1 = \frac{P_{A0}}{(1 - P_{AB} - P_{B0})} \quad \text{i.e. the probability of there being dolphins without herring given the probability of there being no herring}$$

$$p_2 = \frac{P_{B0}}{(1 - P_{AB})} \quad \text{i.e. the probability of there being herring without dolphins given the probability of herring & dolphins not being found together}$$

$$p_3 = P_{AB} \quad \text{i.e. the probability of herring & dolphins being found together}$$

These probabilities were then modelled using Generalised Additive Models (GAMs) with environmental variables (Hastie and Tibshirani 1990, Wood 2000). This method fits non-parametric functions to estimate the relationships between the response (in this case p_i) and the predictor variables, without imposing limitations on the form of the underlying relationships. In this case our environmental variables include latitude, longitude, depth and time category (sunrise 03:00-08:00, morning 08:00-13:00, afternoon 13:00-18:00 and sunset 18:00-23:00). Binomial GAMs with the logit link function were calculated using the MGCV library within R (Wood 2000). Stepwise addition of environmental variables to the null model (of no predictor variables) was carried out, and models compared based on the percentage deviance explained, and UBRE (UnBiased Risk Estimator) score. The UBRE score is the GAM equivalent of the AIC value, and scores on both fit and the number of parameters used to describe the model. The best model for each p_i was selected based on these scores (lowest UBRE score and highest explained deviance), and correlation between variables was evaluated by carrying out Generalised Linear Models (GLMs) on the original dolphin presence/absence and herring presence/ absence data.

The best GAM models were used to generate predicted probability values for p_i and used to calculate the correlation coefficient between dolphins and herring according to the expression (Beare *et al.* 2003):

$$r = \frac{P_{AB} - (P_A \bullet P_B)}{\sqrt{P_A(1 - P_A)P_B(1 - P_B)}}$$

where P_A is the probability of detecting dolphins and P_B is the probability of detecting herring in a segment. Using the modelled p_i , these can be used to calculate P_A and P_B :

$$P_A = p_1(1 - p_2)(1 - p_3) + p_3$$

$$P_B = p_2(1 - p_3) + p_3$$

$$P_{AB} = p_3$$

This method captures the information from the joint distribution (P_{00} , P_{A0} , P_{B0} , P_{AB}), which modelling P_A and P_B directly would miss. The correlation coefficient gives a positive high value (maximum 1) if the species are positively associated with one another (i.e. herring and dolphins present at the same time). A high negative correlation coefficient (minimum -1) suggests that the species are negatively associated with each other (i.e. one species found in a segment when the other is not). This model allows a spatial analysis of association between dolphins and herring.

Results

Survey data

The survey covered shelf waters in the Minch and to the west of the Hebrides and Orkneys from 56°N to 60°N out to the 400 m contour covering a total of 3241 km effective survey track. There were 700 on-transect listening stations each positioned in the middle of the associated 15 minute (2 nmi) herring EDSU segments (Figure 1). Dolphins were detected acoustically throughout the study area in 18.9% of listening stations, whereas herring were detected throughout the study area in 38.9% of the EDSU segments (see Table 1). There were opportunistic sightings of dolphins: mainly white-beaked dolphins (*Lagenorhynchus albirostris*), common dolphins (*Delphinus delphis*) and Atlantic white-sided dolphins (*Lagenorhynchus acutus*). Common and Atlantic white-sided dolphins were found throughout the survey area, whereas white-beaked dolphins were only sighted north of the Outer Hebrides (>59°N).

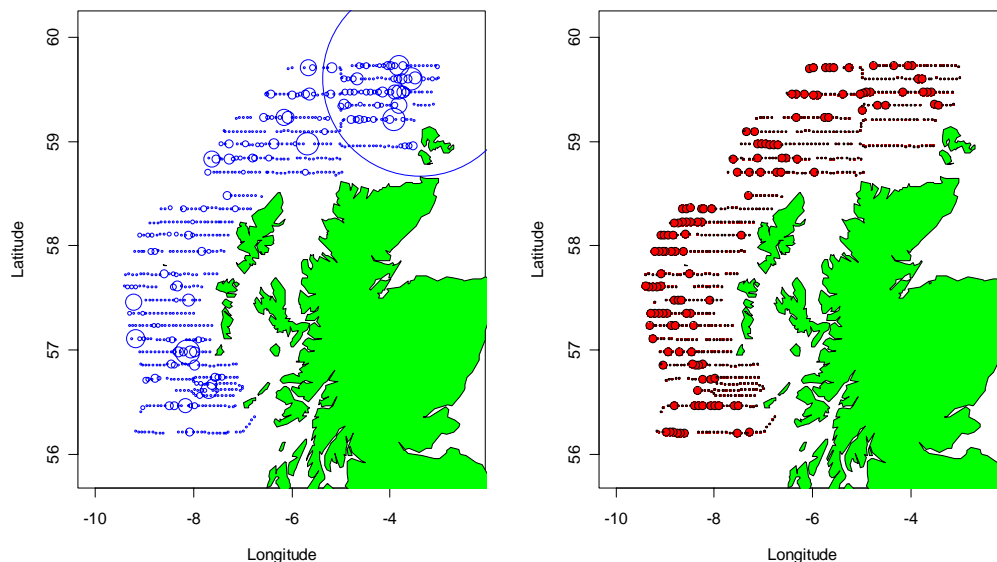


Figure 1 - Maps of the study area in the Northeast Atlantic off the west coast of Scotland. The survey lasting 18 days was carried out in July 2004, and surveyed acoustically for herring (left) and dolphins (right). The locations of the listening stations are shown by small dots, the larger blue circles (left) show the location of herring schools (size of circle related to the square root of the NASC) and the larger red dots (right) show where dolphins were heard. There was one very large school of herring in the north-east of the survey area (NASC = 182913) which is represented by the large blue circle on the map.

Table 1- Summary of the survey effort and parameters included in later analyses. This includes distance surveyed; the number of listening stations and proportion of which had dolphins/ herring; and the range and mean values for the herring NASC and water depth.

Parameter	Value
Survey effort	
Distance surveyed (km)	3241
Survey area (km)	357 x 392
Number of stations/segments	700
Number of stations with dolphins	132 (18.9%)
Number of stations with herring	272 (38.9%)
Herring (NASC)	
Range	0-182913
Median (of non-zero values)	78
Inter-quartile range	28-213
Water depth (m)	
Range	29-490
Mean (standard deviation)	124 (51)

Autocorrelation

The omnidirectional variograms for the dolphin presence/absence data, and the herring presence/absence data are shown in Figure 2. Since the data comprise only presence/absence data, only the effective range (patch diameter) is meaningful. To obtain the effective range exponential models were fitted to the data using an ordinary least squares minimisation with equal weights. From these models the patch diameter was estimated to be 47 km for herring and 90 km for dolphins. This disparity between the two patch diameters may be due to the faster motion of dolphins during the survey than that of the herring.

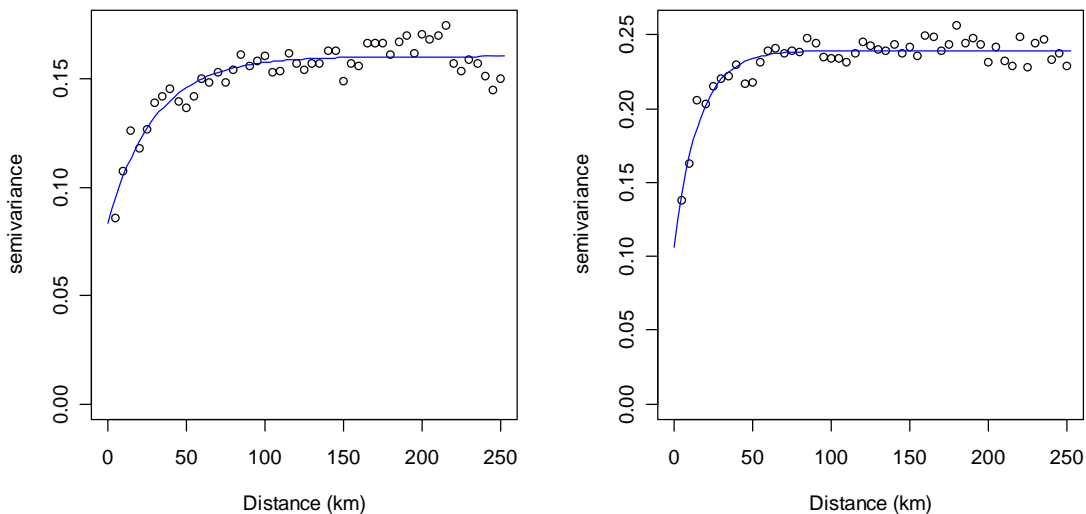


Figure 2 – Omni-directional indicator variograms for (left) the dolphin presence absence data and (right) the herring data: Lag (h) = 5 km \pm 2.5 km (minimum lag = 5km). The exponential model was fitted to the data using an ordinary least squares minimisation with equal weights. The effective range (patch diameter) for the herring model variogram was 47.4 km; and that for the dolphin was 89.7 km.

Temporal autocorrelation is examined within Figure 3, and shows that the data are temporally autocorrelated to 7 segments in dolphins and 8 segments in the herring data. This corresponds to a temporal correlation of around 2 hours (i.e. 37 km within the transect), around half that indicated by the variograms.

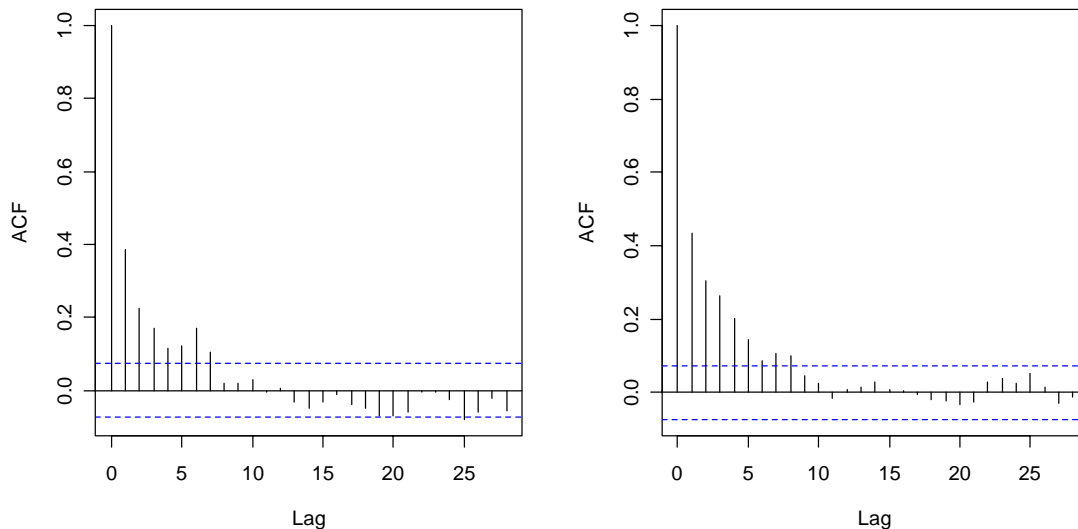


Figure 3 - Autocorrelation function output for presence/absence of dolphins (left) and presence/absence of herring (right). It suggests the data are autocorrelated to 7 segments (32km) in dolphins and 8 segments (37km) in herring.

The results of the spatial and temporal correlation tests gave similar results for herring (30-47 km) but very different results for dolphins (temporal correlation is around half that of spatial correlation). The difference between the results two methods for estimating correlation (higher for spatial than temporal methods) may reflect the speed of movement of the animals through the survey area (giving higher discrepancy for faster moving animals).

Modelling

The results of the generalised additive models suggested that longitude and latitude together were the most important predictors (but not alone). Depth was more important for predicting dolphins than herring presence/absence, whereas time was more important to herring presence/absence. In fact herring detections were significantly different throughout the day, with more herring detections in the middle of the day categories ($p < 0.001$ for the morning category, and $p < 0.01$ for the afternoon category) than during the sunrise and sunset categories (Figure 4). The best models for P_A , P_B , p_1 , p_2 and p_3 are shown in Table 2. Since depth was significantly correlated with longitude ($p < 0.001$), the best models without depth were also chosen, in order to evaluate the influence of depth on the models. Depth improved the fit of all the models except that for p_3 (P_{AB}) suggesting that depth has lesser importance for predicting the presence of both dolphins and herring together.

The results of the GAMs were evaluated by plotting the model with the original data (Figure 5). Dolphins were predicted to occur quite patchily with a small patch in the south of the survey area, a small patch to the west of Uist & Barra, and a larger more continuous patch in the northern part of the survey area (Figure 5). According to the GAM explained deviance, this model is not a bad fit to the data, although there are evidently some clusters of detections left unexplained by the model. On the other hand, the model for herring presence/absence distribution suggests a fairly even distribution throughout the survey area, and appears to

miss some of the finer scale variations in distribution suggested by the original data set. In this case only 32% of the deviance could be explained by the model.

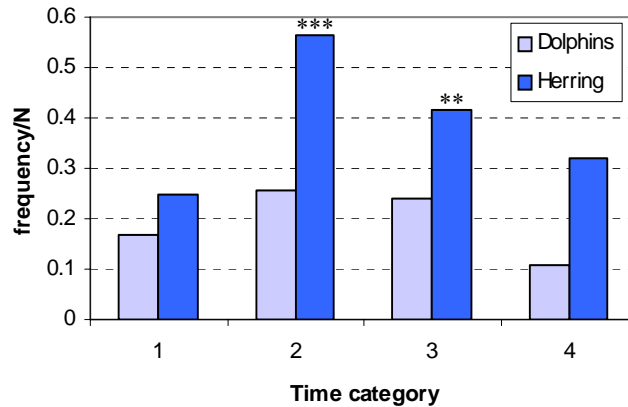


Figure 4 - Histogram of the dolphins and herring per time category, where 1 = 'sunrise' (03:00-08:00), 2 = 'morning' (08:00-13:00), 3 = 'afternoon' (13:00-18:00), 4 = 'sunset' (18:00-23:00). The frequency is divided by the total number of samples in each category. For herring categories 2 & 3 have significantly more herring detections ($p < 0.001$ & $p < 0.01$ respectively).

Table 2 - Summary of the best generalised additive models for predicting P_A (the presence of dolphins), P_B (the presence of herring), and the multinomial logit model probabilities p_1, p_2 and p_3 for each segment. If the 'best' models (selected by highest explained deviance, and lowest UnBiased Ridge Estimator UBRE score) contained a depth term, then the best model without depth has also been summarised. The p-value is the probability that each variable has been included in the model by chance.

Response variable	Model	P value (χ^2)	Deviance explained	UBRE score
P_A	s(Lon,Lat,Time) + s(Depth)		51.6%	-0.278
	s(Lon,Lat,Time)	0.065		
	s(Depth)	<0.01		
P_B	s(Lon,Lat,Time)	<0.05	48.7%	-0.257
	s(Lon,Lat,Time) + s(Depth)		32.0%	0.070
	s(Lon,Lat,Time)	<0.001		
P_1	s(Lon,Lat,Time)	<0.001	30.4%	0.099
	s(Lon,Lat,Time) + s(Depth)		27.1%	-0.279
	s(Lon,Lat,Time)	<0.05		
	s(Depth)	<0.05		
P_2	s(Lon,Lat)	<0.001	23.7%	-0.240
	s(Lon,Lat,Time) + s(Depth)		39.0%	0.030
	s(Lon,Lat,Time)	<0.001		
P_3	s(Lon,Lat,Time)	<0.001	34.5%	0.060
	s(Depth)	<0.001		
	s(Lon,Lat)	<0.01	26.5%	-0.490

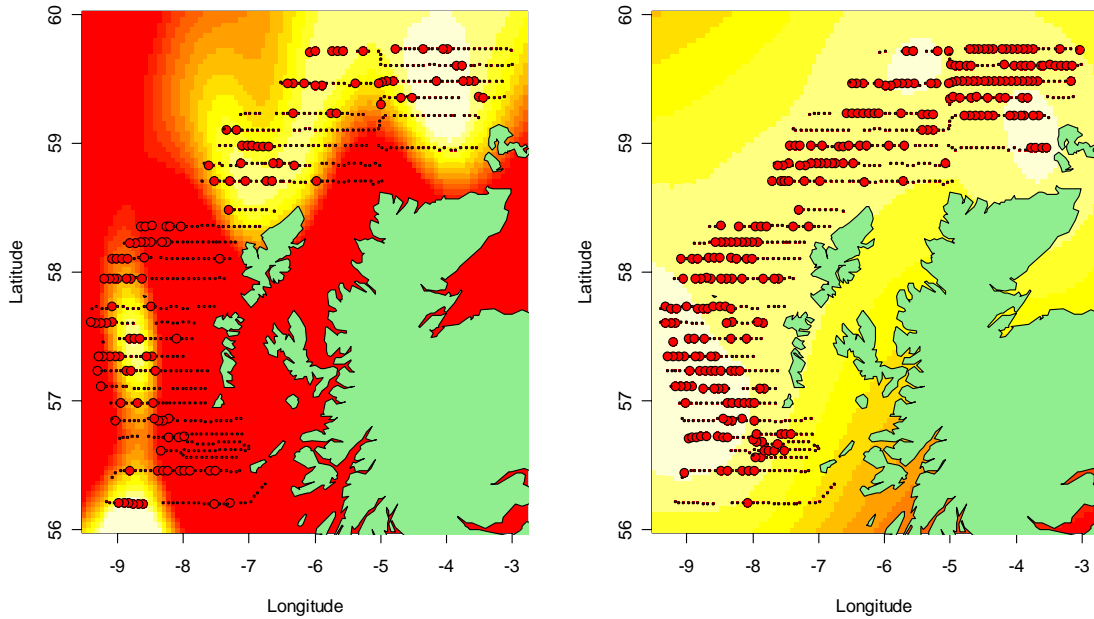


Figure 5 - Prevalence of dolphins (left) and herring (right) estimated using GAMs with smooth terms $s(\text{Lon}, \text{Lat}, \text{Time}) + s(\text{Depth})$. Red is a very low probability of presence, and white is a very high probability of presence. Overlaid are the original data, with large red circles indicating presence.

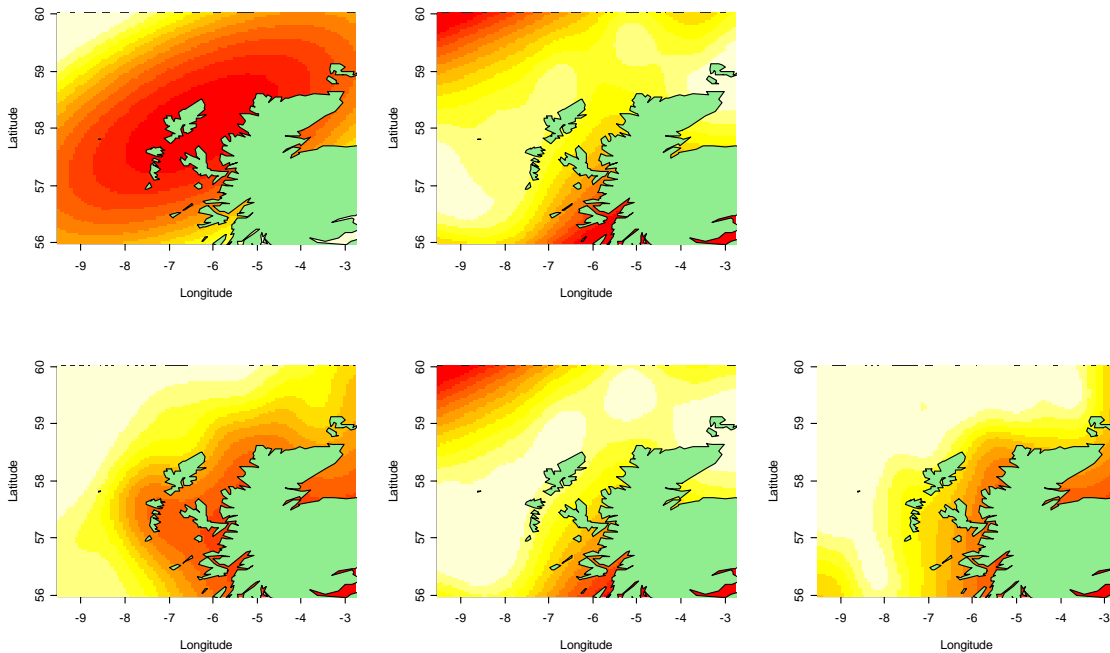


Figure 6 - Predictions for p_1 (left), p_2 (centre) and p_3 (right) of the multinomial logit model based on the binomial GAM $s(\text{Lat}, \text{Lon}, \text{Time}) + s(\text{Depth})$ for p_1 and p_2 in the top panels, and the best models without depth in the bottom panels ($s(\text{Lon}, \text{Lat})$ for p_1 , $s(\text{Lon}, \text{Lat}, \text{Time})$ for p_2 and $s(\text{Lon}, \text{Lat})$ for p_3). Red represents a low probability -> white a high probability for p_i .

Figure 6 plots the best GAM models for the multinomial logit function probabilities p_1 , p_2 and p_3 with the lower panels illustrating the best models excluding depth (except for p_3 which does not have depth as a significant predictor within the model). While removing depth had little influence on the predictions for p_2 (if anything, depth appears to lessen the strength of the prediction), it had a major difference on p_1 (dolphins without herring).

With depth, the model for p_1 predicted a very low probability of dolphins in areas with no herring throughout the survey area. However, without the depth term the model gave a very different result, predicting more dolphins in areas where herring aren't found further from the coast. This suggests that the dolphin's preference for depth was mainly due to the presence of herring. However, when the original data were plotted on top of the predictions, the model without depth appears to fit the data better than the model with depth. Of all the models for p_i , p_2 was the best fit with an explained deviance of 39%, however, when plotted with the original data it is evident that a lot of the finer scale variations in distribution are not captured by the models.

In order to examine the association between the two species, correlation coefficients, r , were calculated using probabilities output from the above GAMs. Since depth was highly correlated with longitude, the correlation coefficients were compared for the best models with depth, and the best models without depth, as shown in Figure 7.

Both models suggested a strong negative correlation between herring and dolphins close to shore, and to the south-west of the survey area. There were positive associations between herring and dolphins towards the shelf edge (where the transects end) but only north and west of Lewis & Harris in both models. Including depth in the models suggested quite an even positive correlation for the majority of the survey area, in particular to the northwest of the survey area. Excluding depth, suggested a much patchier association with positive associations between herring and dolphins occurring in smaller patches.

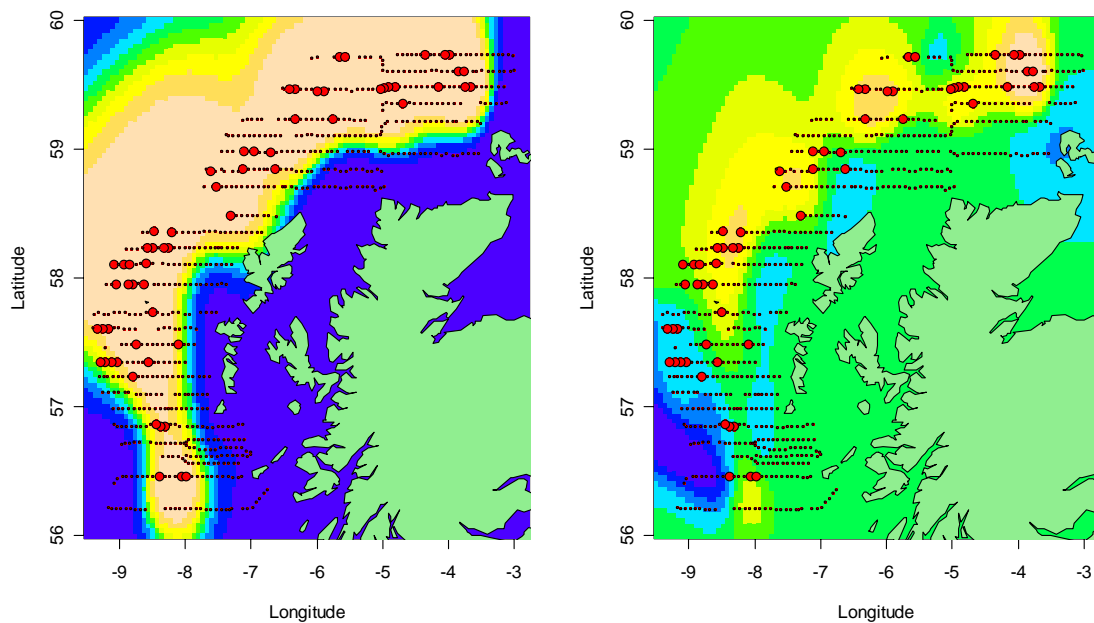


Figure 7 - Spatial variation in correlation between dolphins and herring with (left) GAM models including the depth parameter, and (right) GAM models excluding the depth parameter. Units are correlation coefficients where cold colours (blue) indicate a negative association (i.e. where dolphins and herring are found separately) and warm colours (pink/yellow) indicate a positive association (i.e. where dolphins and herring are found together). Overlaid on the maps is the original data, where a large red dot indicates the presence of both herring and dolphins

Discussion

Passive acoustics is becoming an established method for determining the distribution of some vocalising cetacean species (Leaper *et al.* 1992, Clark and Fristrup 1997, Gillespie 1997, Goold 1998, Gordon *et al.* 2000, Hastie *et al.* 2003, 2005). It is also an ideal method from platforms of opportunity such as the fisheries survey vessels, since it requires a smaller team, and it is affected a lot less by environmental conditions such as sea state and light conditions than visual methods. They also tend to have greater range than visual methods, for example the maximum range of dolphin whistles was estimated to be a little less than 2.5 km (Gordon *et al.* 2000), whereas visual methods have around half this range (maximum). One of the drawbacks with using acoustics for surveying dolphin species is that it is very difficult to identify vocalisations down to species level. There have been a few studies looking at discriminating species from whistles (Steiner 1981, Ding *et al.* 1995, Rendell *et al.* 1999), and it is hoped that in future such methods will allow classification of vocalisations down to species level. However, the main drawback to acoustic surveys for dolphins is the behavioural nature of their vocalisations. Studies show that there are considerable changes in vocalisation rates and patterns with different behaviours (Jones and Sayigh 2002, Cook *et al.* 2004). Jones and Sayigh (2002) found that vocalisation rates in bottlenose dolphins were generally less for feeding than for travelling and socialising. This may seem sensible since some prey species such as herring are able to hear dolphin vocalisations (Wilson and Dill 2002), in addition there is also evidence that dolphins use passive listening to detect prey (Gannon *et al.* 2005) such as herring that are known to produce sound (Wahlberg and Westerberg 2003, Wilson *et al.* 2003), both suggesting dolphins may have a reason for whistling less around prey. However, there are a number of factors that counter such theories: firstly, herring hearing threshold is only within the lower frequencies 100-5000 Hz (Mann *et al.* 2005) so they are unlikely to hear the high frequency dolphin whistles – which are the main vocalisation type used to determine dolphin distribution in this study. Secondly, the species of dolphins found in this study area (common dolphins in particular) tend to feed co-operatively (Young and Cockcroft 1994, Clua and Grosvalet 2001), and are likely to use whistles to communicate with each other. In fact on the recent herring acoustic survey (27 June – 15 July 2005) the author opportunistically sighted a group of common dolphins corralling fish, with numerous feeding seabirds diving in the middle of the feeding dolphins. This sighting was made in the vicinity of the vessel during a trawl on a herring school. Unfortunately, the hydrophone has to be retrieved during trawling, so it was not possible to determine if the dolphins were vocalising during the corralling activity. Since this study uses whistle or echolocation presence/absence rather than whistle rate in the models of distribution, this bias may not be very significant. Diel variations in vocalisations are less of an issue and can be dealt with in the statistical analysis.

The results suggest that dolphins and herring are found throughout the survey area, with white-beaked dolphins concentrated to the north of the outer Hebrides and white-sided and common dolphins found in all areas of the survey region. Dolphins tended to be heard in waters further from the coast, and in the vicinity the shelf edge. The largest aggregations of herring were found in the southern and northern part of the survey area with one very dense school of herring on a steep slope to the north-east of the survey area (ICES 2005). The results of the autocorrelation analysis suggested a smaller patch diameter for herring than for dolphins. In addition, the spatial autocorrelation was larger than the temporal autocorrelation, with the difference being smaller for herring than for dolphins. This disparity may be partly explained by the movement of animals, with dolphins moving faster through the survey area than herring. For dolphins it is unlikely that all of the autocorrelation is due to the detection of the same group of dolphins if they were moving in an unbiased

manner in response to the boat, since previous studies suggested an acoustic range of less than 1.5 nmi (i.e. around half of one section – Gordon *et al.* 2000). However, white-beaked dolphins do show responsive movement to boats (Palka and Hammond 2001), and all three species were observed moving towards the boat and occasionally bowriding. Palka and Hammond (2001) estimated that white-beaked dolphins responded to their vessel from a maximum of 700m, this may contribute towards this autocorrelation to some extent, especially if animals remain with the vessel for long periods of time. Rather than choose a segment size to remove this autocorrelation, the correlation is modelled within the structure of the generalised additive model: Maravelias (1999 & 2001) showed that modelling within a GAM framework on two spatial scales made no difference to the relationships between the herring and the predictor variables. In this study a segment size 15 times larger than the current segment size would have to be used to remove the autocorrelation, which would remove a lot of the spatial variation occurring at scales smaller than the size of their sampling units (Bellehumeur *et al.* 1997).

The models suggested that of all the predictor variables, depth was an important predictor of both dolphins and herring, which is supported by many other studies both for dolphins (Selzer and Payne 1988, Gowans and Whitehead 1995, Davis *et al.* 2002, Baumgartner *et al.* 2001, Canadas *et al.* 2002, Hastie *et al.* 2005), and for herring (Maravelias 1999, 2001). For herring this preference has been linked to the location of the prey species, *Calanus finmarchicus* (Maravelias and Reid 1997, Maravelias 2001). For dolphins it is also believed that this preference for depth is related to the aggregation of prey species (Beardsley *et al.* 1996; Davis *et al.* 2002). This study makes a first step in resolving some of this environmental preference by exploring whether dolphins associate with herring as a prey species. Using latitude and longitude together, however, was a more important predictor than depth. Certainly depth is strongly correlated with longitude, mainly because the shelf edge is at a fairly consistent longitude. However, latitude and longitude together as predictors may summarise many of the environmental factors that influence the distribution of both herring and dolphins, even if it is the environmental factors that are a more direct influence on the animals through biology and ecology. Since the only environmental predictor available in this survey is depth, longitude and latitude provide a useful substitute, even if the models lack strength (most of the models explain less than 30% of the deviance).

Time of day was also an important predictor in many of the models (Table 2), in fact there were significantly more detections of herring during the day than during the sunrise and sunset categories. This is likely to be due to the diurnal behaviour of herring which aggregate in schools close to the bottom during the day (occasionally near the surface), but which disperse into 'scattering layers' at night (as referenced in Maravelias *et al.* 2000). Fernandes *et al.* (2001) showed that this dispersion occurs at sunset, and the schools reform at sunrise.

In addition to this, they showed that school sizes were larger during these times of day, breaking up into more numerous smaller aggregations in the middle of the day. However, the total number of herring was not so influenced by the time of day, as the overall densities were more consistent: i.e. fewer but larger schools were detected prior to dawn and dusk; and more numerous, but smaller schools were detected by day. Time of day also affects the dolphin detection in a similar way to the herring, with more detections during the day than at sunrise and sunset, however this is not statistically significant. There have been several studies that suggest diurnal changes in vocalisation behaviour of dolphins (Goold 2000, Hastie *et al.* 2005). Although in both of these studies, dolphin vocalisations peaked at sunrise and sunset, the reverse to the results of this study. Hastie *et al.* (2005) suggest that this diurnal variation in vocalisation may be related to feeding activity, so it may be that the dolphins in his study were feeding on different species than the dolphins in this study. The

fact that there are more vocalisations during the middle of the day may suggest that the dolphins are feeding on prey that are more available during the middle of the day (such as herring).

The method used by Beare *et al.* (2003) provided a valuable way of exploring an association between herring and dolphins, allowing comparison of the patchy distributions of two species where there are a high proportion of zeros (81% of the dolphin data and 61% of the herring data). Using a simple χ^2 test on the counts of dolphins within the four categories (P_{00} , P_{A0} , P_{B0} and P_{AB}) would throw away all the information available on the spatial distribution of the species. Taking the three probabilities from a multinomial distribution and modelling each of the probabilities within a generalised additive model framework, makes it possible to analyse the correlation between species on both a temporal and spatial scale. The results of the analysis suggest a patchy association of dolphins and herring, with positive association mainly towards the north and north-west of the survey area. A negative association was found close to shore and in the south-west corner of the survey area. This result may reflect a difference in feeding preference for the different species of dolphins – with white-beaked dolphins in the north eating more herring than the common dolphins and white-sided dolphins in the south. There are very few diet studies of dolphins from the west coast of Scotland to confirm foraging preferences of dolphins, mainly because there are very few strandings (and animals from such offshore areas would be unlikely to strand in a fresh condition) and little investigation of bycatch in this area. The most recent diet study in Scottish waters (unpublished data) analysed 9 common dolphins stomachs from Scottish waters and found that the most common prey consumed were mackerel, whiting and herring (25.6%, 18.5% and 13.4% of the estimated prey weight respectively). But very few of the other diet studies either for dolphins within Scottish waters (Santos *et al.* 1994, Santos 1998) or for other dolphins from North Atlantic waters (Overholtz and Waring 1991, Couperus 1997, Reeves *et al.* 1999, Brophy 2003) suggest that common, white-sided or white-beaked dolphins eat substantial amounts of herring. However, all the studies suggest a very opportunistic diet of shoaling fish, for example dolphins bycaught in the mackerel fishery in south-western Irish waters were found with fresh mackerel in their stomachs, also contained otoliths from shoaling mesopelagic fish from deeper waters, suggesting a spatial and temporal change in foraging behaviour (Brophy 2003). So, despite there being little evidence for foraging on herring in the very few diet studies of dolphins in the area, it is unlikely that they feed on this species exclusively. Certainly, in the shelf waters off the west coast of Scotland, herring appeared to be the main shoaling fish available and abundant at this time of year. The visual sighting by the author of common dolphins demonstrating foraging behaviour in the vicinity of a trawl on a known herring school during the last survey also provides some evidence dolphin feeding on herring. This may explain the low level of association between dolphins and herring, in that dolphins feed on herring opportunistically but not exclusively.

The results of the model should, however, be treated with some caution. The accuracy of the correlation coefficient is affected by the accuracy of the predictions from the GAMs. Using only longitude, latitude, time of day and depth results in models that are able to predict at most 39% of the deviance, and generally less than 30%, results in models that miss much of the finer scale detail in the spatial variation. Models that use environmental variables that are more likely to directly influence either of the study species or their prey (such as sea surface temperature, substrate type, location of fronts, etc.) are likely to improve the fit of the models to the data and hence improve the results of the correlation prediction. Such models have been determined for both herring (Maravelias 1999, 2001, Maravelias *et al.* 2000), and for dolphins (Hastie *et al.* 2005, Cañadas and Hammond 2004). During July 2005 the same joint

survey included the collection of Sea Surface Temperature (SST), Sea Surface Salinity (SSS) and substrate type (using Rox-Ann). This data will be used to model herring and dolphin distributions, and to re-assess spatial correlation based on this data for 2005. Future analysis will also include carrying out bootstrapping for variance, to calculate the coefficient of variation (CV) and percentile based 95% confidence intervals for the predictions, and the correlation coefficients.

In conclusion, this study has demonstrated the feasibility of carrying out passive acoustic surveys for dolphins during acoustic fisheries surveys to examine the relationship between dolphins and their prey species. The results of the modelling show that both dolphins and herring are distributed throughout the survey area in large patches, and that depth is the single most important predictor of distribution, based on the limited predictor variables available. There is also a diurnal pattern in both herring and dolphin behaviour. Moreover, dolphins and herring have been shown to be positively associated with each other in some areas, and negatively associated in other areas. This study represents the first attempt at relating dolphins with their prey on a spatial and temporal scale, and provides a modelling framework within which such relationships can be studied. Further improvement of the models with more environmental variables could provide valuable insight into the feeding ecology of dolphins.

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