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Environmental models for predicting oceanic dolphin habitat in the Northeast Atlantic

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Dolphin distributions have been related to a range of oceanographic determinants. The complex topography and hydrography of the Faroe-Shetland Channel have a significant influence on the distribution of many species. However, there is no published detail on how dolphin distributions there are influenced by either topography or hydrography. The study therefore aims to relate dolphin distributions in the Faroe-Shetland Channel to environmental variables, using a general additive modelling framework applied to passive acoustic survey data. Models were created using data from 2001, and were cross-validated to test their predictive power. Predictions were calculated at each stage in the model-building process, and were tested against data from 2002. The results suggest that water noise level, time of day, month, water depth, and surface temperature were significant influences on the probability of detecting dolphins acoustically during 2001. Furthermore, the model was a significant predictor of dolphin distribution in 2002. The model with the greatest predictive power included the terms water noise level, time of day, month, and water depth. The results provide information of potential use in understanding the determinants of dolphin distributions, and hopefully will help managers address concerns about the potential impacts on dolphins of anthropogenic activity.

Keywords: ambient noise, cetacean, diurnal, general additive model, month, passive acoustic, sea surface temperature, surface fluorescence, surface salinity, water depth.

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Introduction

Distributions of dolphins are clearly influenced by their oceanic environment. Although such relationships are inherently dynamic, distributions have been related to a range of environmental determinants, including sea surface temperature (e.g. Selzer and Payne, 1988; Forney, 2000; Baumgartner *et al.*, 2001; Hamazaki, 2002), salinity (e.g. Selzer and Payne, 1988; Forney, 2000), water depth (e.g. Ross *et al.*, 1987; Gowans and Whitehead, 1995; Baumgartner, 1997; Davis *et al.*, 1998), and seabed gradient (Selzer and Payne, 1988; Gowans and Whitehead, 1995; Baumgartner, 1997; Davis *et al.*, 1998). However, the importance of these determinants appears to vary between regions and species, a feature that highlights the need to focus studies on the role of oceanography in dolphin habitat selection on a regional basis.

Recent and historical data suggest that parts of the Northeast Atlantic may provide an important habitat for a number of cetacean species (Thompson, 1928; Brown, 1976; Evans, 1980; Gunnlaugsson and Sigurjónsson, 1990; Weir *et al.*, 2001). Visual surveys have recorded significant numbers of white-sided dolphins (*Lagenorhynchus acutus*) throughout the area (Skov *et al.*, 1995; Weir *et al.*, 2001), and they are thought to be the most abundant species of dolphin in the region (Harwood and Wilson, 2001). Recently, more than 20 000 white-sided dolphins were estimated for a small region of the Northeast Atlantic: the

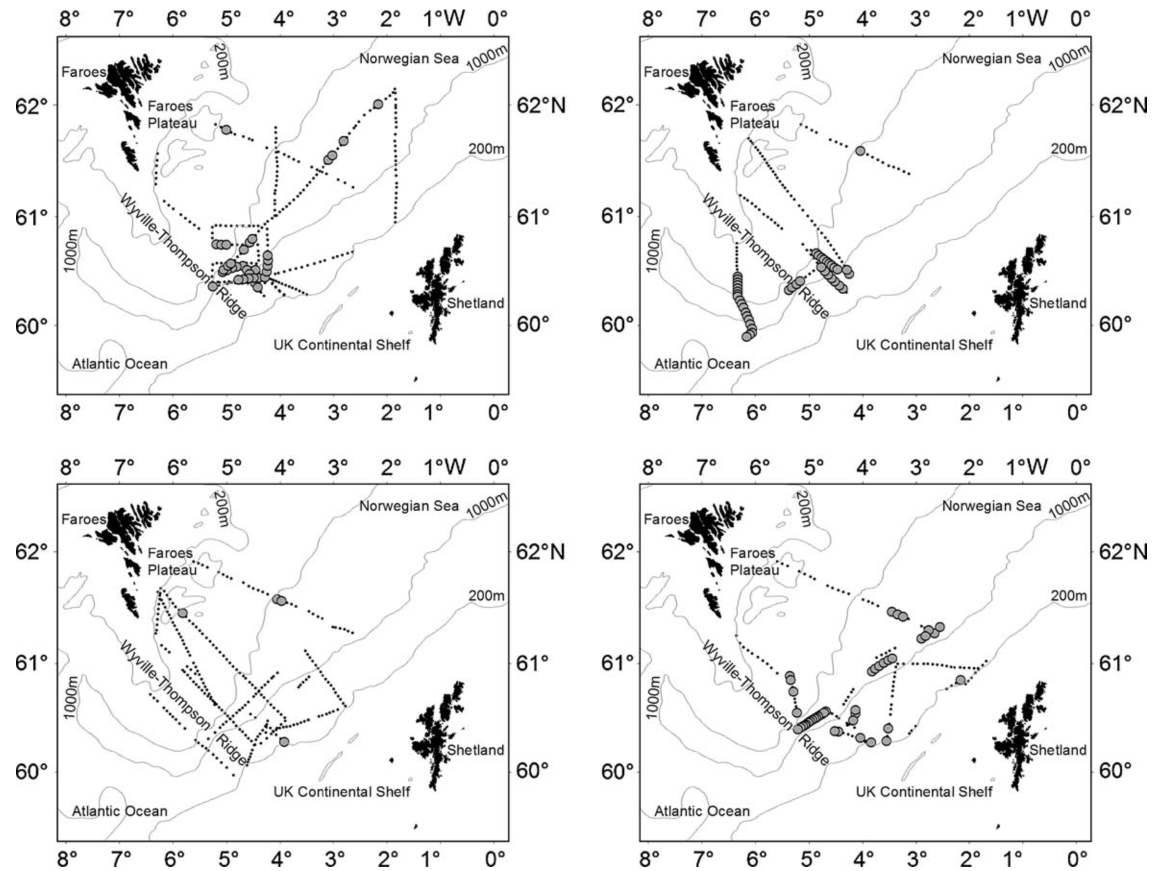

Figure 1. Maps of the study area in the Northeast Atlantic showing the Faroes and Shetland Islands. Surveys lasting 14 days were carried out in May (top left) and October (top right) 2001 and May (bottom left) and October (bottom right) 2002, to build and test environmental models for predicting dolphin distribution in this region. The locations of the acoustic listening stations are shown by the black dots, and the locations where dolphins were heard are shown by the larger grey dots. The dashed contour lines represent water depths of 200 m and 1000 m.

Faroe-Shetland Channel (Hughes *et al.*, 1998). Observations of dolphins were made throughout the year, and the species was most abundant in deep water along the shelf edge (Weir *et al.*, 2001).

The Faroe-Shetland Channel encompasses part of the UK continental shelf and Faroese plateau, and is intersected by a channel approximately 1500 m deep that runs northeast through the area. At its northern entrance, the channel is connected to the Norwegian Sea; at its southern end, the Wyville-Thompson ridge runs perpendicular to the channel, and there is a connection over the ridge with the Northeast Atlantic Ocean (Turrell *et al.*, 1999; Figure 1). The hydrographic regime of the Faroe-Shetland Channel is extremely complex, and it has long been recognized as an important conduit connecting the warm waters of the Atlantic with the cold waters of the Nordic seas (Sherwin *et al.*, 1999). The complex topography and the dynamic hydrography of the area appear to have a significant influence on the distribution and abundance of many species (Bett, 2001), but there are currently no details on how environmental factors influence the distribution of dolphins in the channel. Therefore, to understand the role of environmental determinants in the ecology of dolphins in the area, systematic data on the distribution of dolphins need to be collected in parallel with detailed oceanographic information. Such data should provide the basis for developing environmental models, with a flexibility suitable for examining relationships between dynamic oceanographic variables and complex, often patchy, distributions of animals. The models should aim to have both within-year explanatory value and interannual predictive power, to ensure that the pertinent variables are correctly identified and that distribution−environment relationships are consistent between years. This information is important, both in understanding the determinants of oceanic dolphin distributions, and in helping to address concerns about potential impacts from increasing numbers of anthropogenic activities in the region (Harwood and Wilson, 2001).

The initial aim of this study was to evaluate the distribution of oceanic dolphins in the Faroe-Shetland Channel. We also seek to relate the distribution patterns of dolphins to environmental variables and to the underwater topography of the area, and then to build environmental models that describe dolphin distribution in this region. Finally, we undertook a series of formal tests to determine whether the models were capable of predicting dolphin distribution interannually.

Material and methods

Passive acoustic surveys for dolphins were carried out in the Faroe-Shetland Channel during 2-week oceanographic cruises in May and October 2001 and October 2002 from the FRV "Scotia", a 68 m oceanographic research vessel, and in May 2002 from the FRV "Cirolana", a 73 m oceanographic research vessel.

Dolphin data collection

The acoustic equipment used to detect dolphins consisted of a towed stereo hydrophone streamer, an amplification and filtering unit, and a computer for making recordings. The hydrophone was specially designed and built for the project, but was based on systems developed in previous studies (Leaper *et al.*, 1992; Hastie *et al.*, 2003). The streamer consisted of two Benthos AQ4 elements with individual preamplifiers (Magrec, Devon, UK), mounted 3 m apart in a 10 m, oil-filled, 1-inch diameter polyurethane tube. The preamplifiers had a low-cut filter designed to provide −3 dB at 100 Hz to limit low frequency tow and water noise. The system was otherwise flat to 15 kHz, and had good sensitivity to well above the 22 kHz upper limit of the computer sound card. The streamer was towed on a 400 m strengthened cable behind the vessel. At speeds of 10 knots, this design of array generally tows at around 5−6 m below the surface (Gillespie, 1997). For retrieval and storage, the cable and streamer were coiled onto the main net drum winch situated centrally above the aft deck of the vessels. A 60 m extension cable was connected to the tow cable once it was deployed, to connect the array to recording equipment located within the vessel's laboratories.

Signals from the hydrophones were filtered using high-pass filters set at 400 Hz or 1600 Hz, depending on ambient noise conditions, amplified by 20 dB or 30 dB using a custom-built differential amplifier/filter unit. The data logging software package *Logger 2000* (Gillespie, 1997) ran in real time throughout the surveys and maintained a database of monitoring effort, recordings, and acoustic detections.

A two-person team worked in shifts to monitor the signals from the hydrophone 24 h a day. A series of listening stations was established at 15-min intervals along the survey track. At each station, the signals from the hydrophones were monitored carefully for 1 min, and the presence or absence of dolphins was recorded. In addition, a qualitative assessment of the strength, from 0 (absent) to 5 (high), of the following acoustic information was recorded to a database using the *Logger 2000* software: survey vessel noise, water noise, and remote ship noise. The geographic location of each listening station was recorded in the database using a Global Positioning System (GPS) unit (Garmin GPS 75, Garmin Ltd). Visual watches for cetaceans were maintained on an opportunistic basis to identify species detected acoustically. The distribution of listening stations, together with information on acoustic detections of dolphins made during the surveys, was mapped using a Geographic Information System (GIS) software package (Arcview version 3.2, ESRI Inc.).

Environmental data collection

Surface water temperature and salinity were recorded continuously throughout the surveys using a Sea-Bird SBE 21 thermosalinograph connected to the vessels' non-toxic seawater supply. Surface water fluorescence was also recorded throughout the surveys using a SeaTech fluorometer, giving an indirect measure of phytoplankton concentration measured in $\mu g\,l^{-1}$. The nominal output signal from the fluorometer was converted to estimates of chlorophyll *a* using a linear calibration calculated from chlorophyll *a* concentrations in water samples collected by scientific personnel (FRS Marine Laboratory, Aberdeen, UK) throughout the surveys. Simultaneous navigation data were recorded from a GPS navigation system. Depth and seabed gradient were estimated for each listening station using a digital elevation model, interpolated from satellite-derived altimetry data (available from http://topex.ucsd.edu/marine_topo/mar_topo.html; Smith and Sandwell, 1997). The digital elevation model was created in a GIS package (Arcview, version 3.2, ESRI Inc.) using an inverse distance-weighted algorithm. The derived depths were compared with water depth recorded by the survey vessels' echosounders (Simrad EK-500) and were not significantly different from the echosounder depths (paired t-test; $t = -0.41$, d.f. $= 719$, $p = 0.679$).

Data analyses

The relationship between dolphin occurrence and oceanographic variables was examined within a generalized additive modelling framework (Hastie and Tibshirani, 1990) applied to data from listening stations along the survey track. Such models fit non-parametric functions to estimate the relationships between response and predictor variables, without imposing limitations on the form of the underlying relationships.

The occurrence of dolphins at each of the listening stations was considered independent. This was based on the fact that at the vessels' slowest cruising speeds of around 10 knots, each station would have acoustic overlap at a radius of 2.3 km. This is likely to be further than dolphins could be detected using the equipment in this study (Gordon *et al.*, 1998). The presence or absence of dolphin calls at each listening station was based on the acoustic information recorded in the field with the *Logger 2000* software. Only data from the 2001 surveys were used to construct the environmental model.

Presence or absence of dolphins was analysed by specifying a binomial distribution of errors with a logit link function. Models were selected and evaluated by first fitting each variable to the null model. The term that resulted in the greatest improvement in the model fit was selected for inclusion at the next step. At each successive step, all remaining variables were again tested individually for possible inclusion. The significance of each variable was evaluated with an analysis of deviance. A level of smoothing corresponding to 3 degrees of freedom was chosen for variables, because it permits non-linear effects yet restricts unrealistic detail in the shape of the curve. This allows for the detection of major effects, but reduces spurious patterns or potential sampling artefacts (Forney, 2000). Cubic smoothing splines were used to estimate the functions (Hastie and Tibshirani, 1990).

To account for those variables that were unlikely to affect the presence of dolphins at a listening station but could potentially affect the probability of detecting them, the variables in the model were initially entered in a series of blocks. Variables were selected for inclusion in the model using a stepwise procedure, first fitting each variable in the ambient noise block (water noise, survey vessel noise, remote ship noise) to the null model. The term that resulted in the greatest improvement in the model fit was selected for inclusion at the next step. At each successive step, all remaining variables in the block were again tested individually for possible inclusion. When all significant variables were added to the model from the ambient noise block, variables from the temporal block (time of day and month), and then the environmental block (surface temperature, surface salinity, surface fluorescence, water depth, seabed gradient), were similarly tested for inclusion in the model. To ensure that the term "time of day" was biologically meaningful, and to ensure that the term was consistent between survey months, each 24-h period was subdivided into eight categories, four between sunrise and sunset, and four between sunset and sunrise, and each listening station was allocated to its corresponding category. Mean sunrise and sunset times were calculated for each survey using a computer-based sunrise–sunset calculator available from http://www.sunrisesunset.com/sun.html. All analyses were carried out using the software package SPLUS 2000 (Mathsoft Inc.).

To test the predictive power of the resultant model, a cross-validation approach was used. Each time a significant term was included during the 2001 model-building process, response predictions based on the data collected during the 2002 surveys were calculated (using the coefficients of the 2001 model). This allowed us to monitor how well the 2001 model fitted the 2002 data, as terms were added and the model became progressively more complex. Essentially, these predictions consisted of a probability of detecting dolphins at each 2002 listening station, based on the acoustic, temporal, and environmental information at that listening station. These predicted probabilities were then tested against the observed occurrence of dolphins from the 2002 data using generalized linear models with a logit link function (i.e. logistic regression). Tests for evidence that the predicted probabilities effectively fitted the observed occurrence were based on the application of likelihood ratio tests, with p-values computed using a χ^2 approximation. In addition, the kappa coefficient was evaluated for each stage of the model-building process. This is a performance measure that assesses the predictive power of a model on the basis of the number of correct and incorrect predictions of presence or absence. Each of the predicted values from the model in this current study has a probability value between 0 and 1, and presence of dolphins was accepted at a threshold probability of 0.5 (Manel *et al.*, 2001). The model from the 2001 data that provided the best predictor of the 2002 data was identified as the "best prediction" model.

Results

Survey data

Survey coverage in the Faroe-Shetland Channel was extensive, a total of 3482 km being covered and 779 listening stations occupied during the four cruises (Figure 1). Survey tracks were generally longer during May than during October, and more listening stations were established in May.

The oceanographic environment differed between cruises: mean surface temperature was generally higher during October than May ($F = 652.4$, d.f. = 3, $p < 0.0001$), mean surface salinity was highest during May 2002 and at a minimum during October 2002 ($F = 779.9$, d.f. = 3, $p < 0.0001$), and mean surface fluorescence peaked during October 2002 and was at a minimum during October 2001 ($F = 86.07$, d.f. = 3, $p < 0.0001$). The range of water depths and seabed gradients surveyed during each of the cruises also varied significantly (water depth, $F = 29.34$, d.f. = 3, $p < 0.0001$; seabed gradient, $F = 5.92$, d.f. = 3, $p = 0.001$).

Dolphins were detected acoustically throughout the study area during each survey. The proportion of listening stations where dolphins were detected varied from 0.02 during May 2002 to 0.34 during October 2001 (Table 1). Three schools of dolphins were sighted during opportunistic watches from the vessels' bridge; two were Atlantic

Table 1. Summary of survey effort and environmental variables during the 2001 and 2002 surveys. Details include the distance surveyed, the number of listening stations monitored, the number of stations where dolphins were heard, and the range and mean values for surface temperature, surface salinity, surface fluorescence, water depth, and seabed gradient.

	2001		2002	
Parameter	May	October	May	October
Survey effort				
Distance surveyed (km)	1 193	599	1 057	633
Number of listening stations	256	125	247	151
Stations with dolphins	36 (14%)	42 (34%)	4 (2%)	43 (29%)
Environment				
Surface temperature (°C)				
Range	7.9–12.3	9.7–12.3	8.1–10.9	10.9–13.1
Mean (s.d.)	9.5 (0.5)	10.9 (0.7)	9.8 (0.7)	12.0 (0.4)
Surface salinity				
Range	35.01–35.24	34.97–35.29	35.12–35.56	34.83–35.19
Mean (s.d.)	35.27 (0.05)	35.18 (0.07)	35.35 (0.07)	35.02 (0.07)
Surface fluorescence ($\mu g\, l^{-1}$)				
Range	141–6 882	639–1 418	294–3 494	1 961–2 818
Mean (s.d.)	1 430 (1 232)	889 (184)	1 303 (647)	2 422 (144)
Water depth (m)				
Range	204–1 639	204–1 302	200–1 302	202–1 333
Mean (s.d.)	929 (379)	711 (383)	642 (334)	742 (336)
Seabed gradient (°)				
Range	0.17–3.14	0.18–2.86	0.17–5.46	0.00–3.25
Mean (s.d.)	0.86 (0.60)	0.85 (0.68)	1.03 (0.72)	0.73 (0.74)

white-sided dolphins and one remained unidentified as it was too far from the vessel to identify the species.

Environmental model

The results of general additive modelling suggest that several variables were significant influences on the probability of detecting dolphins during 2001. Specifically (in order of selection), the model included water noise level, time of day, month, water depth, and surface temperature.

Of the ambient noise level indices, only water noise level was a significant influence on the detection of dolphins during 2001 (Table 2). Detections peaked at water noise levels of 1 and 4, and were at a minimum at a level of 2. Although the relationship was non-linear, as background water noise increased, the probability of detecting dolphins generally decreased (Figure 2). The levels of survey ship noise and remote ship noise were not significant influences on the detection probability of dolphins (Table 2).

Both time of day and survey month were significant influences on dolphin detections during 2001 (Table 2). Throughout the day, dolphin detections remained relatively consistent. However, there was a marked drop in detections during the period immediately before sunset (Figure 2). Although the number of dolphin detections was clearly higher during October than May (Table 1), the inclusion of water temperature in the model revealed that much of this monthly variation in detection rate could be explained by a positive relationship with water temperature at the surface (Figure 2).

Two of the environmental variables showed significant relationships with dolphin distribution during 2001, water depth and surface temperature (Table 2). Detections showed a non-linear relationship with water depth, peaking in depths of 750–1100 m, and were at a minimum in shallow depths around 200 m, the depth at which sampling started (Figure 2). There was a positive relationship between surface temperature and dolphin distribution during 2001, detections peaking at 12 °C and at a minimum at temperatures of 8 °C (Figure 2).

The model created using 2001 survey data was a significant predictor of the distribution of dolphins in 2002 at several stages in the model-selection procedure. However, the model that provided the "best prediction" of the 2002 data, as determined from the logistic regression analyses (Table 3, Figure 3) and the kappa coefficients

Table 2. Summary of the general additive model for predicting the occurrence of dolphin calls at listening stations during 2001. Variables were selected for inclusion in the model using a stepwise procedure by first fitting each variable in the ambient noise block to the null model. The term that resulted in the greatest improvement in the model fit was selected for inclusion at the next step. At each successive step, all remaining variables in the block were again tested individually for possible inclusion. When all significant variables were added to the model from the ambient noise block, variables from the temporal block and then the environmental block were similarly tested for inclusion in the model.

Term added to model	Deviance	d.f.	p (χ^2)
Ambient noise			
Water noise level	31.06	3.0	<0.0001
Survey ship noise level	6.75	4.0	0.149
Remote ship noise level	6.72	4.0	0.15
Temporal			
Time of day	41.04	7.0	<0.0001
Month	18.17	1.0	<0.0001
Oceanographic			
Water depth	23.38	2.0	<0.0001
Surface temperature	8.93	2.0	0.012
Surface salinity	1.97	2.0	0.36
Seabed gradient	1.17	1.9	0.519
Surface fluorescence	0.94	1.9	0.59

(Table 3), included the terms water noise, time of day, month, and water depth.

Discussion

The study has provided quantitative data on the oceanic distribution of dolphins in the Faroe-Shetland Channel. Moreover, we believe we have demonstrated clear and predictable influences of environmental determinants on the distributions of dolphins in the region.

The use of passive acoustics to study the distribution or abundance of vocal animals such as dolphins is now recognized as a highly efficient monitoring technique (Leaper *et al.*, 2001; Van Parijs *et al.*, 2002). Such techniques offered several advantages over traditional sighting surveys; acoustic range is generally greater than visual range, and acoustic detection probability is likely to be less affected by environmental conditions at the surface. In addition, when at the surface, dolphins are often difficult to see. In the context of a project aiming to achieve year-round coverage in the Northeast Atlantic, an area where seas are often rough and winter days are short, these advantages are important. One of the drawbacks with using just acoustic data to map dolphin distribution is that oceanic dolphins are difficult to identify to species level, and it remains possible that some acoustic detections were of schools of different or mixed species. However, previous studies suggest that the most common species of dolphin in the region are white-sided dolphins, with other species such as white-beaked dolphins (*Lagenorhynchus albirostris*) generally being found shallower than 200 m (Weir *et al.*, 2001) and common dolphins (*Delphinus delphis*) generally occurring farther south than the Faroe-Shetland Channel (Evans, 1980). The visual sightings made in the current study lend support to this statement, and it seems likely that most of the acoustic detections were of white-sided dolphins. In future, more detailed analyses of whistle features may allow discrimination between many species (Rendell *et al.*, 1999).

The results support previous studies showing that dolphins are widespread throughout the offshore regions of the Northeast Atlantic (Evans, 1992; Weir *et al.*, 2001). We have demonstrated that patterns of distribution are closely linked to the bathymetric regime within the area. The use of general additive models provided a flexible framework that allowed the development of environmental models to identify predictive variables without the constraints of assumptions about the underlying relationships. The results suggest that many of the relationships between environmental determinants and dolphin distributions are non-linear and, as such, it is possible that they would not have been detected or would have been misinterpreted using other methods of analysis that rely on assumptions about the underlying relationships.

The model created using the data collected during 2001 suggests that water noise level, time of day, survey month, water depth, and surface temperature are all significant predictors of dolphin distribution. However, as a result of the flexibility of GAMs, there is a possibility of overfitting the data (Forney, 2000), resulting in misinterpretation of distribution–environment relationships from a single year's data.

The model does appear to have a reasonable degree of predictive power, with several stages in the model-building process being significant predictors of the 2002 data. However, some of the variables that explained within-year patterns of dolphin distribution during 2001 turned out to be poor predictors of distribution between years. This was likely the consequence of spurious within-year patterns that do not represent true ecological relationships. The "best prediction" model, or the one that proved to be the best predictor of the 2002 data, contained the variables water noise level, time of day, month, and water depth. Landis and Koch (1977) suggested that a kappa coefficient around the value found in this current study (0.56) indicates a model of "good" performance. Therefore, it would seem reasonable to assume that the environmental variable in this model (water depth) has the greatest influence on dolphin occurrence in the region.

Previous studies have shown that water depth is a significant factor in determining the distribution of air-breathing

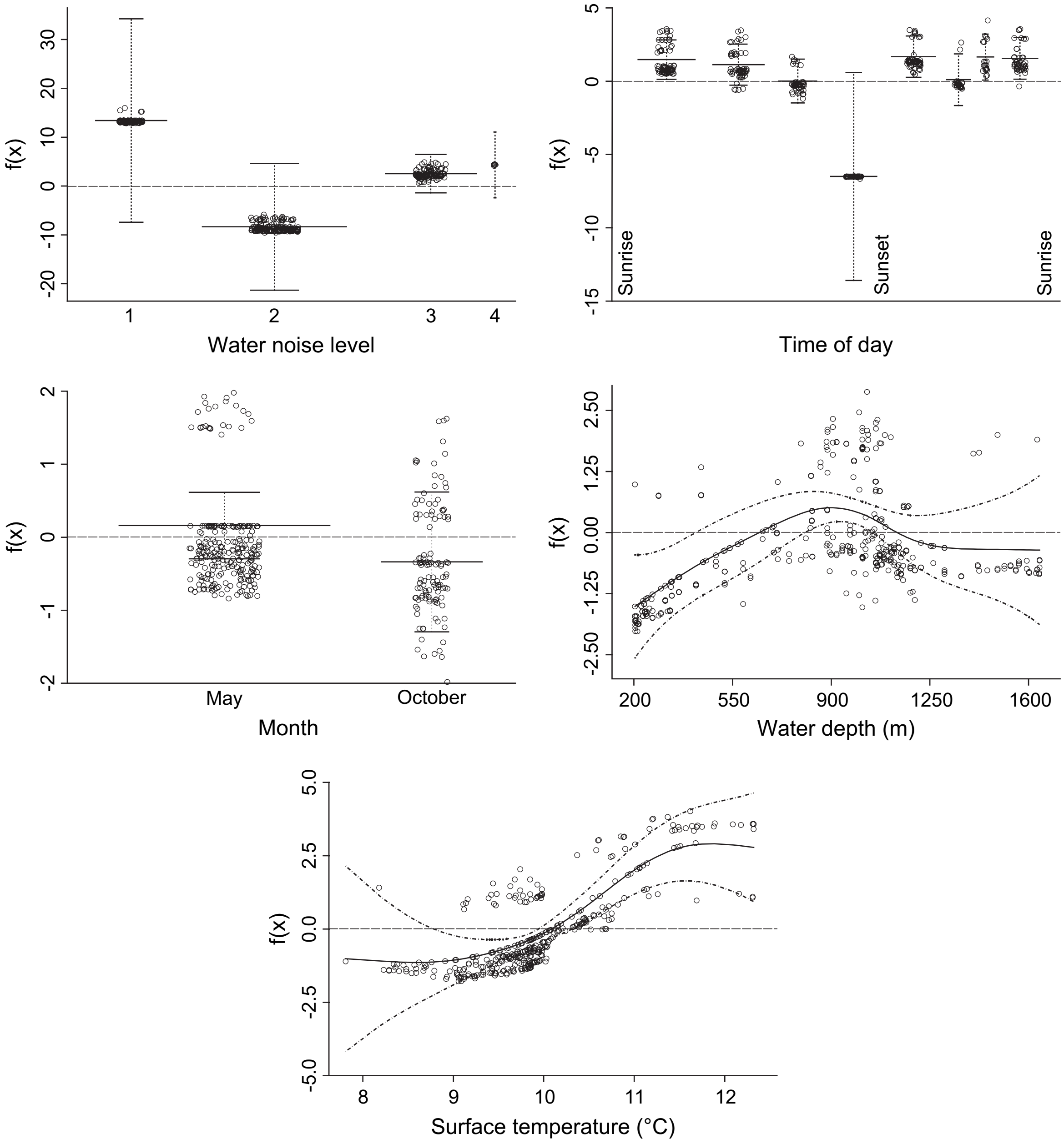

Figure 2. Generalized additive model functions of dolphin encounter rates in relation to environmental variables. The "best prediction" model is at the stage when water noise, time of day, month, and water depth are included. Functions are scaled to the model mean. The dashed lines represent two s.e. bands. The horizontal dashed line represents f(x) = 0.

marine species (e.g. Selzer and Payne, 1988; Baumgartner, 1997; Schneider, 1997; Raum-Suryan and Harvey, 1998). Although varying in their detail, all hypotheses relate water depth to the availability of prey. With limited information on the distribution of fish species within the study area, it is difficult to make precise links between predator and prey distributions. However, a study of the stomach contents of white-sided dolphins west of Ireland revealed that the most common fresh prey item in stomachs were mackerel (*Scomber scombrus*; Couperus, 1997). This is a species that makes a southward spawning migration along the fringes of the shelf edge between October and March (Reid *et al.*, 1997). Although survey effort in the current study was limited to May and October, previous studies suggest

Table 3. The predictive power of the 2001 environmental models. Using the terms of the 2001 model, model response predictions, based on the data collected during the 2002 surveys, were calculated at the inclusion of each term in the model-building process. These predictions, consisting of a probability of detecting dolphins at each 2002 listening station, based on the ambient noise, and temporal and environmental information at that listening station, were tested against the actual occurrence of dolphins from the 2002 data using generalized linear models with a logit link function. In addition, the predictive power of the model was tested using the kappa coefficient. The model from the 2001 data with the greatest predictive power was identified as the "best prediction" model and is shown by an asterisk.

Term	Coefficient	s.e.	Deviance	d.f.	p (χ^2)	Kappa
+ Water noise level	−1.66	1.78	0.867	1	0.352	0
+ Time of day	0.69	1.61	0.809	1	0.368	0
+ Month	6.97	1.16	44.19	1	<0.0001	0.19
+ Water depth	7.32	0.87	100.9	1	<0.0001	0.56*
+ Surface temperature	5.8	0.77	93.89	1	<0.0001	0.46

that dolphins are most commonly sighted from late summer through to November in the region (Weir *et al.*, 2001). However, as our surveys were limited to water depth >200 m, decreases in detection probability during different survey months could potentially represent inshore movements by dolphins during those months (Northridge *et al.*, 1997), making direct comparisons with other studies difficult.

In addition to water depth and month, time of day was a significant influence on the probability of detecting dolphins. Owing to the geographical extent of the survey effort, this pattern is unlikely to be a result of variations in distribution throughout the day. It is more likely that the result is a consequence of diurnal variations in vocal activity of dolphins. Such behaviour has been recorded previously in common dolphins in the Irish Sea (Goold, 2000). Moreover, the diurnal patterns of activity in Goold's study are markedly similar to the variations in detection probability with time of day in the current study; activity peaking during the early morning and late at night. Goold (2000) suggested that this behaviour might reflect an increase in vocal communication caused by the lack of visual cues at night, or diurnal patterns in feeding activity. Alternatively, variations in dive depth (Mate *et al.*, 1995) or temperature characteristics of the vertical water column throughout the day may also account for the observed patterns of detection probability.

Intuitively, it might be expected that variations in ambient noise levels would prove to be strong determinants of our ability to detect dolphins during surveys. It was surprising, therefore, that the variables that described the ambient noise during the surveys (water noise, survey vessel noise, remote vessel noise) were relatively poor predictors of dolphin detections. Further, the relationship between dolphin detections and the only significant acoustic variable, water noise level, proved to be inconsistent between years. It is clear, however, that factors such as the use of acoustic filters to limit low frequency noise, and variations in survey vessel speed resulting in variations in the depth of the hydrophone array, further complicate any underlying relationships between ambient noise and the probability of detecting dolphins.

Although water temperature was a significant predictor of dolphin occurrence in 2001, it is of note that the hydrographic regime of the study area was a relatively poor predictor of distribution between years. This is in contrast to previous studies that suggest that surface water temperature and salinity can be used as good predictors of dolphin occurrence (e.g. Selzer and Payne, 1988; Forney, 2000; Baumgartner *et al.*, 2001; Hamazaki, 2002). However, the hydrography of the Faroe-Shetland Channel is highly complex, with up to five water masses occupying the area and mesoscale eddies travelling north through it (Sherwin *et al.*, 1999). The areas described in many previous studies (Forney, 2000; Gregr and Trites, 2001; Hamazaki, 2002) may be more stable both temporally and spatially, allowing relationships with hydrography to develop.

Alternatively, complications in the relationships between dolphin detections and surface temperature or surface salinity in the current study are introduced owing to the inherent effects of water temperature and salinity on the speed of sound in seawater (Urick, 1967). This may have the result that potential ecological links between dolphins and temperatures or salinities were masked or distorted as a consequence of variations in detection probability with these variables.

In conclusion, this study has utilized passive acoustic techniques from oceanographic research vessels to map the distribution of dolphins in the Faroe-Shetland Channel, and has related them to environmental variables. The results of the modelling procedures show that dolphins are distributed widely in the area, and that water depth is the most robust environmental predictor of their distribution between years. Moreover, dolphins showed a distinctive seasonal change in relative abundance, and a diurnal pattern in vocal behaviour. The models therefore provide important new information in understanding the determinants of oceanic dolphin habitat in the Northeast Atlantic, and provide a valuable tool to help managers address concerns about potential impacts from anthropogenic activity. Further studies would benefit from being focused on refining the habitat predictions and examining relationships between dolphin distributions and environmental correlates over periods of several years. Valuable insights into the long-term role of oceanography and topography on top predators could then result, and these could potentially be used to support monitoring the biological aspects of the changing oceanographic regime in this important area.

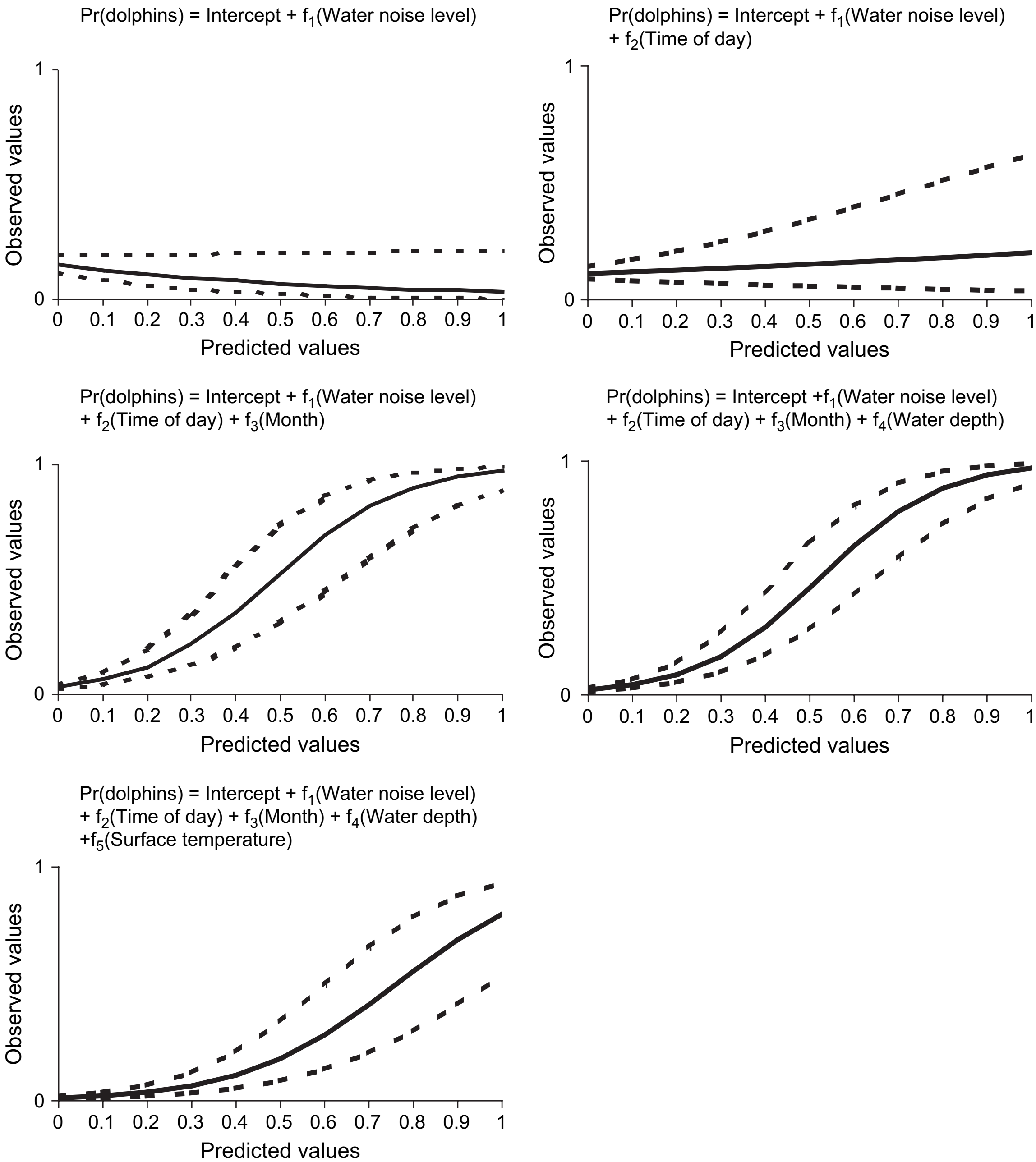

Figure 3. Logistic functions (±s.e.) that represent the relationships between the predicted and observed values of dolphin occurrence, as each term is included to produce a progressively more complex model. The terms included in the model at successive steps are water noise level, time of day, month, water depth, and surface temperature. The "best prediction" model is at the stage when water noise, time of day, month, and water depth are included.

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