

Article

Oceanographic Drivers of Cuvier's (*Ziphius cavirostris*) and Sowerby's (*Mesoplodon bidens*) Beaked Whales Acoustic Occurrence along the Irish Shelf Edge

Cynthia Barile ^{*} , Simon Berrow  and Joanne O'Brien 

Marine and Freshwater Research Centre (MFRC), Galway-Mayo Institute of Technology (GMIT), H91 T8NW Galway, Ireland; simon.berrow@gmit.ie (S.B.); joanne.obrien@gmit.ie (J.O.)

* Correspondence: cynthia.barile94@gmail.com

Abstract: Cuvier's and Sowerby's beaked whales occur year-round in western Irish waters, yet remain some of the most poorly understood cetaceans in the area. Considering the importance of the area for anthropogenic activities and the sensitivity of beaked whales to noise, understanding their ecology is essential to minimise potential overlaps. To this end, fixed bottom-mounted autonomous acoustic recorders were deployed at 10 stations over four recording periods spanning from May 2015 to November 2016. Acoustic data were collected over 1934 cumulative days, for a total of 7942 h of recordings. To model the probability of presence of Cuvier's and Sowerby's beaked whales in the area as a function of oceanographic predictors, we used Generalised Additive Models, fitted with Generalised Estimating Equations to deal with temporal autocorrelation. To reflect prey availability, oceanographic variables acting as proxies of primary productivity and prey aggregation processes such as upwelling events and thermal fronts were selected. Our results demonstrated that oceanographic variables significantly contributed to the occurrence of Cuvier's and Sowerby's beaked whales (p -values between <0.001 and <0.05). The species showed similar preferences, with the exception of sdSST. The inclusion of a parameter accounting for the recorders location confirmed the existence of a latitudinal partitioning for those species in the area. This study provides a point of comparison for future research and represents an important step towards a better understanding of those elusive species.

Keywords: beaked whale; *Ziphius cavirostris*; *Mesoplodon bidens*; oceanography; acoustics; western Ireland; deep diving cetaceans



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1. Introduction

Beaked whales (*Ziphiidae*) represent the second most diverse family of toothed whales (Odontoceti), currently comprising at least 23 species in six genera [1], with a potentially new species recently suspected off Mexico (Barlow 2020, unpublished). Beaked whales species occur worldwide, occupying deep, typically offshore pelagic waters, and show preferences for topographically complex areas [2,3], driven by the occurrence of deep-water cephalopod species on which they primarily prey [4,5]. They perform long and deep dives in pursuit of their preys, with very short surfacing intervals [6,7]. Due to these habitat preferences and elusive behaviour, beaked whales are challenging to observe from traditional platforms, hampering research efforts. In the rough offshore waters of the northeast Atlantic, visual encounter rates are often too low for robust species-specific investigations to be undertaken [8].

Beaked whales are acoustically active during their deep foraging dives, making passive acoustic monitoring (PAM) techniques particularly useful and valuable [9]. More specifically, static bottom-mounted instruments have the capacity to monitor for extended periods of time, at a lower cost than boat-based techniques and are more likely to detect deep divers' clicks given their potential operating depth. Beaked whales are the only

odontocete species to emit frequency modulated clicks [10]. The spectral characteristics of Cuvier's [10,11] and Sowerby's beaked whales [12] (focal species of this study) have been previously described in the literature and their uniqueness allow reliable species discrimination.

The slopes of the Irish Atlantic Margin, an area comprising waters to the west of the continental shelf, is an ideal candidate habitat for beaked whales, interspersed with canyons and troughs [13]. Together with a complex topography, the area is subject to complex oceanographic and hydrographic processes which combined, make it one of the most biologically productive regions in the northeast Atlantic [13]. Frontal systems, large eddies, upwelling and downwelling conditions have been recorded in the area [14–16]. Such events enhancing the local productivity propagate through the foodweb and determine the availability of prey items and in turn the occurrence of larger predators [13]. Many cephalopod species have indeed been recorded in the region [17,18], offering feeding opportunities to beaked whale species.

Out of six beaked whale species recorded in the northeast Atlantic, five have been reported in Irish waters to date. Northern bottlenose and Cuvier's beaked whales are the most frequently sighted and stranded species [19] and some speculate that the latter might be breeding in Irish waters [20]. Sowerby's beaked whales (*Mesoplodon bidens*) have been sighted and found stranded on multiple occasions, but the recent sightings of calves during a survey on the shelf edge strongly suggest that Sowerby's beaked whales could be breeding in the area [19]. True's beaked whales (*Mesoplodon mirus*) have been identified in more than a dozen stranding events with individuals of different sizes, including a mother and a calf [21] but are likely to have been sighted at sea on a single occasion only [13]. Gervais' beaked whales (*Mesoplodon europaes*) are known from a single stranding [22]. Finally, Baird's beaked whales stranded on two occasions in UK waters but have not yet been recorded in Ireland [19].

Despite the diversity of the beaked whale family, we still know relatively little on many species. Most of the long-term research efforts have been focused on four species [2], including multiple populations of Cuvier's (*Ziphius cavirostris*) and Blainville's beaked whales (*Mesoplodon densirostris*) [23–25], as well as single populations of northern bottlenose (*Hyperoodon ampullatus*) [26] and Baird's beaked whales (*Berardius bairdii*) [27]. For other species, information often relies on beach-cast individuals or skeletal remains [28,29]. Beaked whales, as all other cetacean species, are listed under the Annex IV of the European Union (EU) Habitats Directive (EU-COM, 1992), entitling them to a strict level of protection. However, "to implement meaningful species conservation measures under the Directive, a good knowledge of each species (range, occurrences, biology, ecology, threats and sensitivity, conservation needs, etc.) is a *conditio sine qua non*" [30]. Enhancing the knowledge on distribution, abundance, habitat use and sensitivity to relevant threats can therefore be considered a priority.

The lack of information on beaked whales is even more alarming given that they have been identified as sensitive to anthropogenic noise [25,31,32]. In particular, mid-frequency military sonar exposure has been blamed in many atypical mass stranding events [33–35] and shown to induce behavioural changes [25,36,37]. Although much less studied, other intense sound sources such as shipping and seismic airguns are of concern [34,38,39]. In 2018, the western Irish and British coasts experienced the largest unusual mortality event of beaked whales recorded globally. While causes of death could not be confirmed, lesions were not inconsistent with acoustic traumas [40]. Three similar stranding events of a lesser magnitude have occurred in the area over a decade [40,41]. The Irish Atlantic Margin is thought to hold significant hydrocarbon resources, placing the area at the frontline of increased noise levels, with seismic prospects expected to multiply [42]. It becomes evident that investigating the spatio-temporal overlap between beaked whales and such anthropogenic stressors is important to devise strategies to manage and minimise potential risks.

Here, we used data collected along the Irish Atlantic Margin over two years using bottom-mounted recorders to examine the occurrence of foraging Cuvier's and Sowerby's beaked whales, in relation to oceanographic drivers susceptible to influence the distribution of prey items. Direct prey-related information is generally difficult to access and environmental variables acting as proxies are often used instead [43] and allow an indirect examination of the habitat preferences of predators [5,44,45]. Little is known about the influence of oceanographic variables on the presence of Cuvier's and Sowerby's beaked whales. This study explores the largest acoustic dataset collected using static devices in Europe to date, to provide information on factors which could influence the presence and distribution of those elusive species.

2. Materials and Methods

2.1. Data Collection

Acoustic data were collected along the edge of the continental shelf off western Ireland using Autonomous Multichannel Acoustic Recorders (AMARs; JASCO Applied Sciences) over four recording periods spanning from May 2015 to November 2016 (Table 1). The devices were suspended 15 m above the seafloor at four locations in 2015 (M1–M4) and six in 2016 (M3, M5–M9; Figure 1 and Table 1), at an average operating depth of approximately 1800 m.

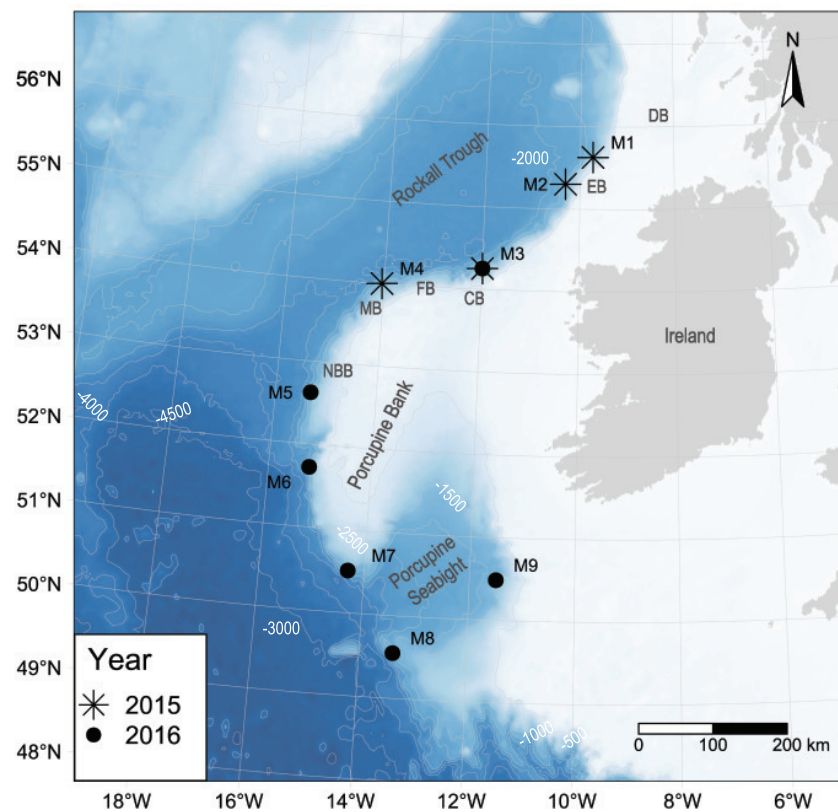


Figure 1. Location and year of deployment of the AMARs deployed along the Irish Atlantic Margin. CB: Colm Basin, DB: Donegal Basin, EB: Erris Basin, FB: Fursa Basin, MB: Macdara Basin, NBB: North Brona Basin.

Table 1. Location, depth, operation period, daily and overall recording durations of AMARs deployed at nine stations off western Ireland in 2015 and 2016.

Mooring	Latitude (°N)	Longitude (°W)	Depth (m)	Start	End	Recording Duration Per Day (Hours)	Recording Period (Cumulative Days)	Total Recording Time (Hours)
M1	55.6302	−9.7302	1600	8 May 2015	22 August 2015	6.5	214	1391
	55.6323	−9.7252	1620	29 August 2015	13 December 2015	6.5		
M2	55.3018	−10.3084	1995	8 May 2015	22 August 2015	6.5	214	1391
	55.3011	−10.3037	1971	29 August 2015	13 December 2015	6.5		
M3	54.2513	−11.9940	1850	30 August 2015	14 December 2015	6.5	107	696
	54.2502	−11.9926	1770	24 March 2016	29 June 2016	2.6		
M4	54.0014	−14.0424	1920	7 May 2015	20 August 2015	6.5	212	1378
	54.0015	−14.0429	1944	30 August 2015	13 December 2015	6.5		
M5	52.6225	−15.3045	1752	21 March 2016	10 July 2016	2.6	227	590
	52.6221	−15.3046	1750	10 July 2016	2 November 2016	2.6		
M6	51.7226	−15.2077	1765	20 March 2016	11 July 2016	2.6	210	546
	51.7245	−15.2342	1745	11 July 2016	15 October 2016	2.6		
M7	50.5096	−14.3124	1750	19 March 2016	11 July 2016	2.6	230	598
	50.5085	−14.3150	1750	11 July 2016	3 November 2016	2.6		
M8	49.5477	−13.3730	1760	19 March 2016	9 August 2016	2.6	122	598
	49.5478	−13.3723	1760	9 August 2016	3 November 2016	2.6		
M9	50.4867	−11.4963	1530	2 June 2016	4 November 2016	3.2	156	499

In 2015, AMARs were equipped with omnidirectional HTI-99-HF hydrophones (High Tech Inc., Harrison County, MI, USA, -164 dB re 1 V/ μ Pa sensitivity), operating on 8-min duty cycles and recording for 130 sec during each cycle. In 2016, omnidirectional M36-V35-100 hydrophones (GeoSpectrum Technologies Inc., Canada, -165 dB re 1 V/ μ Pa sensitivity) were used, operating on 8-min or 15-min duty cycles, with recording durations of 64 to 97 s per cycle. To record high-frequency beaked whale clicks, high sampling rate channels (250 kHz) with a 16-bit resolution, a spectral noise floor of 35 dB re 1 μ Pa²/Hz and a nominal ceiling of 171 dB re 1 μ Pa were used. The instruments were retrieved using acoustic releases and recordings stored on internal solid-state flash memory.

2.2. Beaked Whale Detections

To identify odontocete clicks, acoustic recordings were processed using the combination of a custom automated click detector and classifier developed by JASCO Applied Sciences [46]. The algorithm is based on the zero-crossings in the acoustic time series (i.e., the rapid oscillations of clicks above and below the signal's normal level). Firstly, a high-pass filter was applied to the raw data to remove the energy below 8 kHz. This allows the energy from cetacean clicks to pass while removing that of other sources such as cetacean tonal calls, shrimps and vessels. A Teager-Kaiser energy detector [47] was then applied, to detect potential clicks. For each detected click, three classification parameters were extracted: (1) the number of zero-crossings within the click, (2) the median time separation between zero-crossings and (3) the slope of the change in time separation between zero-crossings. This last parameter is particularly helpful for beaked whales, which clicks can be identified by a frequency increase (i.e., upswEEP). Those parameters were compared to a beaked whale click template library and Mahalanobis distances [48] were computed (i.e., the characteristics of recorded clicks were compared to typical distributions of click characteristics). Each click was classified as the species which corresponded the lowest value.

To verify the performance of the automatic detector, experienced bio-acoustic analysts carried out a visual and aural review of a selection of acoustic files using PAMlab (JASCO Applied Sciences). To be representative, the selection process was standardised, covering various conditions (i.e., time of year and day, number of automatic detections, number of species detected). The identification of beaked whale clicks was based on previous descriptions available in the literature [10–12]. The validation process evaluated the performance of the automatic detector in identifying at least one click in an acoustic file, but did not indicate whether all or only a portion of the recorded clicks were detected. To compare the manual and automatic detection results, a maximum likelihood estimation algorithm was used to determine the detection threshold, i.e., the minimum number of automated detections necessary for a species to be considered as present in the investigated file, that maximised the *F*-score (*F*), calculated as follows:

$$F = \frac{(1 + \beta^2)P * R}{(\beta^2)P + R}; P = \frac{TP}{TP + FP}; R = \frac{TP}{TP + FN} \quad (1)$$

where the precision (*P*; proportion of accurate detections) and recall (*R*; proportion of recorded clicks automatically detected) indices are calculated based on the proportion of clicks correctly identified (true positives; *TP*), incorrectly identified (false positive; *FP*), or missed (false negatives; *FN*). Hence, presence/absence data were used and the species of interest was considered absent in acoustic files in which the number of automatic detections failed to meet the detection threshold. The procedure carried out has been described thoroughly by Kowarski et al. [46]. Precision was prioritised over recall throughout the process to maximise the reliability of the results.

2.3. Environmental Variables

The selected oceanographic variables were comprised of chlorophyll a concentration (chl_a in mg/m³), standard deviation of sea surface temperature (sdSST in °C), mean relative SST (relSST in °C) and sea surface height (SSH in m). Static variables (e.g., depth, slope aspect) were not relevant in this study because of the lack of variability inherent to the use of static recorders. As means to account for latitudinal differences in detection rates, “mooring ID” was included as an additional variable.

The chl_a concentration was selected as an indicator of primary productivity and phytoplankton biomass at the surface. Data was gathered by the Moderate Resolution Imaging Spectroradiometer (MODIS) aboard NASA’s Aqua Spacecraft and accessed from NOAA CoastWatch program website (<http://coastwatch.pfeg.noaa.gov/index.html>, accessed on 2 February 2021) using the R [49] package ‘rerddapXtracto’ [50]. Given the predatory nature of beaked whale cephalopod preys, a temporal lag of about 3 to 4 months is expected for peaks in primary productivity to translate into increases in cephalopod biomass [44,45,51]. Hence, daily mean chl_a concentration was averaged over the 90 days preceding each recording date [44,45].

The sdSST and relSST were used as proxies for frontal activity and upwelling, respectively, processes influencing the availability and concentration of cephalopods [44,45]. We used SST data from the Pathfinder Version 5.3 dataset, collected by the Advanced Very High Resolution Radiometer (AVHRR) aboard NOAA’s Polar Operational Environmental Satellites (POES) and pre-processed by the NASA’s SeaWiFS Data Analysis System (SeaDAS). The relSST was calculated as the difference in SST between each recording station and the average across the study area (defined as 52.5°–57° N, 9°–17° W in 2015 and 48°–56° N, 11°–17° W in 2016) for the corresponding month. Finally, we used SSH data from the HYCOM (HYbrid Coordinate Ocean Model) data assimilative system. SST and SSH data were accessed from NOAA CoastWatch program website using the R package ‘rerddapXtracto’.

Choosing an arbitrary scale to investigate the significance of environmental processes can lead to contradictions, given that relationships between top predators and environmental features depend on the scales considered [51]. To work around this issue, we preferred a multi-scale approach, by which variables were tested under different spatio-temporal scales. For SSH data, both weekly and monthly averages were considered at spatial resolutions of 0.25 × 0.25° and 0.50 × 0.50°. Due to missing values in SST data, monthly averages only were evaluated for sdSST and relSST, at different spatial scales (0.20 × 0.20°; 0.30 × 0.30° and 0.50 × 0.50° for Cuvier’s beaked whales, 0.10 × 0.10°; 0.20 × 0.20°; 0.30 × 0.30° and 0.50 × 0.50° for Sowerby’s beaked whales). Those same spatial scales were considered for chl_a. The finest spatial resolution at which the covariates were considered was of 0.10 × 0.10° and 0.20 × 0.20° for Sowerby’s and Cuvier’s beaked whales, respectively. This decision related to the maximum detection range of the signals of interest in the area, predicted to be smaller for Sowerby’s (4 km) than for Cuvier’s beaked whale clicks (14 km) [19,46]. Relationships between detections and environmental conditions could be concealed if detection ranges exceed the scale of analysis [52].

2.4. Data Analysis

To investigate the relationships between the oceanographic parameters described above and Sowerby’s and Cuvier’s beaked whales presence/absence (response variable), we used a generalised additive model (GAM) framework [53]. To this end, presence/absence data and values for the environmental variable of interest were associated with each single acoustic file (recorded every 8 min to 15 min) and input into a single model for each species, all sites combined. Although investigating relationships on a site-by-site basis would have been ideal to eliminate potential bias associated with the location of each recorder, the lack of variability in oceanographic variables at each individual site did not allow such a fine-scale analysis. To counteract this limitation and account for spatial differences in detection rates in this data shown by Kowarski et al. (2018) [46], “mooring

ID" was added to the models as a categorical variable. All steps of data visualisation and analysis were performed using scripts in R (version 4.0.3 [49]).

GAMs are widely used in modelling cetacean habitat and distribution, and allow the investigation of non-linear cetacean-habitat relationships by replacing linear functions of the covariates by smoothing functions [43,54]. However, significant temporal autocorrelation of the residuals was revealed here by autocorrelation function plots and represents a violation of GAM assumptions. To address this issue, we have used generalised estimating equations (GEE), following the methodology in Pirotta et al. (2011) [45] to obtain so-called GEE-GAMs. This strategy consists of grouping successive data points in independent blocks and fitting a correlation structure within each block [55]. The temporal dependence is expected to decrease with time, so an autoregressive order-1 (AR-1) covariance structure was used here [56]. Multicollinearity between explanatory variables was tested using the variance inflation factor (VIF). Binomial GEE-GLMs (generalised linear models) with a log-link function were fitted using the R library 'geepack' [57]. The 'splines' library was used to incorporate B-splines, thus extending to a GEE-GAM. All environmental covariates were tested either as linear terms or as 1-dimensional smooth terms (4 degrees of freedom), modelled as cubic B-splines with one internal knot at the average value of the covariate. The categorical variable "mooring ID" was tested as a factor.

To select the best subset of variables, the quasi-likelihood under independence model criterion (QIC) [58] was used to compare models in a stepwise selection. Model selection can not be undertaken including the covariates under all their spatial and temporal scales due to their strong collinearity. Thus, each variable was first tested at its different spatio-temporal scales against the response variable to retain a single, optimal scale to be included in the full model. This procedure resulted in comparing the QIC score of a null model with those of a series of models containing the variable of interest at each of its available scales. Once the most appropriate scale (spatial and temporal) and form (linear or smooth) were found, a full model containing all selected covariates was fitted. A backwards stepwise model selection was carried out by fitting a series of reduced models with all variables but one. Covariates were taken out step by step, until none could be further removed without increasing the QIC score. To determine the significance of each remaining covariate, successive Wald's tests were then carried out on the final model. Non-significant covariates were removed one by one until all those remaining were significant ($p < 0.05$).

To evaluate model performance, presence-absence confusion matrices summarising the model's goodness-of-fit were used [59]. To build a confusion matrix, a cut-off probability value has to be selected, beyond which a prediction is considered a presence. To select an appropriate cut-off, a Receiver Operating Characteristic (ROC) curve plotting the proportion of correctly classified presences (i.e., sensitivity) versus the proportion of incorrectly classified presences (i.e., specificity) was computed using the R library 'ROCR' [60]. The best cut-off was identified as the point where the distance between the ROC curve and a 45° diagonal is maximised. In addition, the area under the curve (AUC) was computed ('ROCR' library) to assess overall model performance (the closer the AUC is to 1, the better the model [61]).

To visualise the contribution of the predictors, partial residual plots of the estimated relationships between the response and each of the variables were computed using the R library 'ggplot2' [62] and R-scripts coded by Pirotta et al. (2011) [45].

3. Results

3.1. Detector Performance

To verify the performance of the automatic click detectors, experienced analysts manually reviewed 2830 acoustic files (1.09% of recordings) [46,63]. Across M1 to M8 the Cuvier's beaked whale click classifier had a precision of 0.87 and a recall of 0.79 (F -score = 0.86, Table 2). At M9, the recall value (0.80) was higher than the precision (0.48), requiring the implementation of a classification threshold, which substantially optimised the precision (post-threshold precision = 1, Table 2).

The performance of the Sowerby’s beaked whale click classifier was also satisfactory, yielding a precision of 0.96 and a recall of 0.57–0.93 (F -score = 0.85–0.95, Table 2). It did not require any optimisation because the precision was already higher than the recall, which was our priority.

Table 2. Detector performance in detecting (recall, R) and correctly classifying (precision, P) beaked whale clicks. Data from [46,63].

Species	Mooring ID	P	R	Classification Threshold	$P^{\text{optimised}}$	$R^{\text{optimised}}$	$F^{\text{optimised}}$
Cuvier’s	M1–M8	0.87	0.79	1	0.87	0.79	0.86
	M9	0.48	0.80	7	1.0	0.30	0.68
Sowerby’s	M1–M8	0.96	0.93	1	0.96	0.93	0.95
	M9	0.96	0.57	1	0.96	0.57	0.85

3.2. Scale Selection

Explanatory variables were tested for multicollinearity, but VIF values remained below 2 which allowed us to proceed and evaluate all four environmental variables of interest in our models. Following our multi-scale approach, the appropriate spatial and temporal scales (when appropriate) were selected for each oceanographic variable, taking each species separately. As a result, chl a and SSH data were retained on the $0.50 \times 0.50^\circ$ scale, sdSST on the $0.20 \times 0.20^\circ$ scale and relSST on the $0.30 \times 0.30^\circ$ scale (Table 3) in the case of Cuvier’s beaked whales.

Table 3. Spatio-temporal scales under which chl a concentration (mg/m 3), sdSST ($^\circ\text{C}$), relSST ($^\circ\text{C}$) and SSH (m) were retained for Cuvier’s and Sowerby’s beaked whale.

Species	Covariate	Scale Selected	Covariate Median (Range)
Cuvier’s	chl a	$0.50 \times 0.50^\circ$ -90 days	0.66 (0.18 to 1.3)
	sdSST	$0.20 \times 0.20^\circ$ -Monthly	0.19 (0.00 to 0.46)
	relSST	$0.30 \times 0.30^\circ$ -Monthly	0.22 (−2.9 to 2.7)
	SSH	$0.50 \times 0.50^\circ$ -Weekly	−0.51 (−0.65 to −0.35)
Sowerby’s	chl a	$0.30 \times 0.30^\circ$ -90 days	0.62 (0.18 to 1.3)
	sdSST	$0.20 \times 0.20^\circ$ -Monthly	0.19 (0.00 to 0.46)
	relSST	$0.50 \times 0.50^\circ$ -Monthly	0.17 (−2.9 to 2.8)
	SSH	$0.25 \times 0.25^\circ$ -Monthly	−0.51 (−0.61 to −0.41)

With regards to the temporal scales, weekly SSH averages were retained, while monthly averages were retained for sdSST and relSST. For Sowerby’s beaked whales, chl a was retained on the $0.30 \times 0.30^\circ$ scale and SSH on the monthly $0.25 \times 0.25^\circ$ scale. Similarly to Cuvier’s beaked whales, monthly sdSST averages on the $0.20 \times 0.20^\circ$ scale were retained, but relSST was retained at a coarser spatial resolution of $0.50 \times 0.50^\circ$.

3.3. General Observed Trends

Acoustic data were collected at four stations in the northern half of the shelf edge of the Porcupine Bank from late spring (May) to early winter (December) 2015. Another five stations were monitored in 2016 from early spring (March) to late fall (November) in the southern half of the shelf edge of the Porcupine Bank and in the Porcupine Seabight (Figure 1 and Table 1). Exceptionally, M3 was monitored in 2016 due to equipment failure in the first half of the sampling period in 2015. This represented a temporal coverage of 447 days in total, across both years. Across all stations, 1790 cumulative days were acoustically monitored. This resulted in a total of 7942 h of recordings from which click detections of Cuvier’s and Sowerby’s beaked whales were extracted. Cuvier’s and Sowerby’s clicks were detected in 2.6% and 1.1% of the total number of recordings ($n = 260,210$) and during 96% and 95% of the days monitored across both years ($n = 447$), respectively. Boxplots were

generated to visualise the ranges of the oceanographic variables of interest (under their appropriate spatio-temporal scales—see Table 3) observed in both the absence and presence of beaked whale click detections (Figure 2). Ranges and medians for those explanatory variables are also given in Table 3.

When Cuvier’s beaked whale clicks were detected, observed values of chl_a were lower than in the absence of detections (median = 0.49 mg/m³ vs. 0.65 mg/m³, respectively). The opposite tendency was observed for Sowerby’s beaked whales, with higher chl_a values in the presence of click detections (median = 0.68 mg/m³) than in their absence (median = 0.62 mg/m³). Monthly averages of relSST were higher in the presence of Cuvier’s beaked whale click detections (median = 0.26 °C) than in their absence (median = 0.17 °C). The opposite trend occurred with Sowerby’s beaked whale clicks, with lower monthly relSST (median = 0.014 °C) in the presence than in the absence of detections (median = 0.17 °C). For both species, the values of sdSST were very similar in the absence or presence of click detections (median = 0.19 °C). Finally, there was no noticeable difference in SSH in the presence or absence of Cuvier’s beaked whale click detections (median = −0.52 m). Regarding Sowerby’s beaked whales, the presence of click detections seemed to be associated with lower SSH values (median = −0.54 m) than their absence (median = −0.51 m).

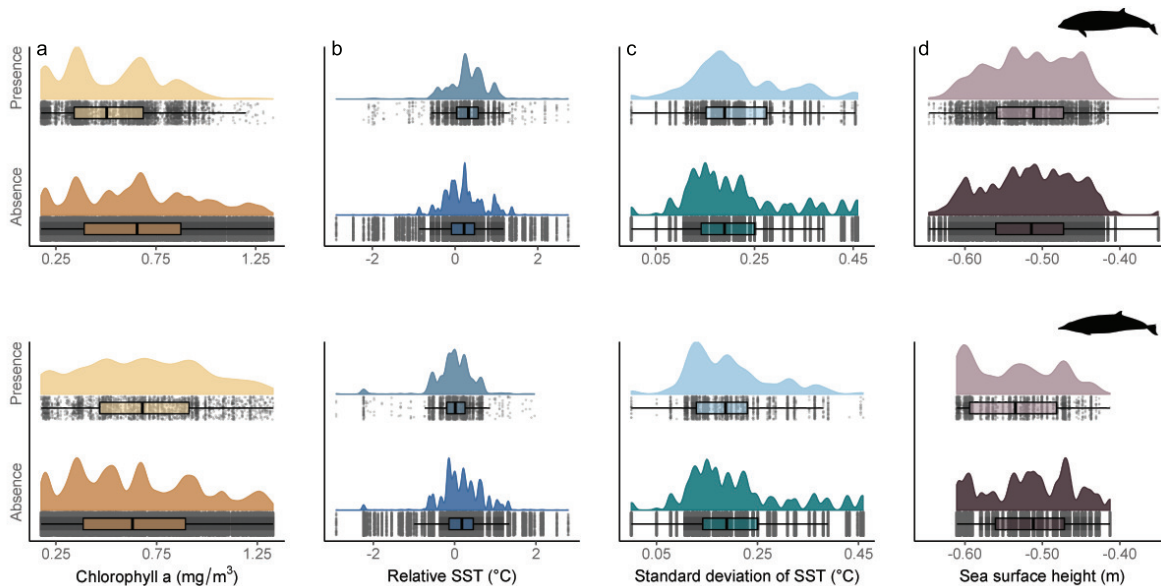


Figure 2. Observed values of oceanographic variables in the presence and absence of Cuvier’s (first row) and Sowerby’s (second row) beaked whale click detections: (a) chl_a concentration, (b) relative sea surface temperature (SST), (c) standard deviation of SST and (d) sea surface height. Each variable is shown at the most appropriate scale, as determined by the preliminary multi-scale approach (see Table 4).

3.4. Modelling Results

For Cuvier’s beaked whales, all oceanographic variables considered (chl_a, sdSST, relSST and SSH) were retained as smooth terms (i.e., non-linear). The subsequent covariate selection process, based on QIC scores and then on Wald’s tests, retained as final the model containing all covariates which were considered, namely chl_a, sdSST, relSST, SSH and mooring ID (*p*-values in Table 4). The confusion matrix suggested a capacity of the model to correctly predict 83% of the presences and 60% of the absences, for an AUC of 0.77.

Table 4. Summary of model performance (AUC) and Wald’s test results for all significant covariates in the final models. The order in which covariates are listed reflects their importance in the models.

Species	AUC	Covariate	χ^2	<i>p</i> -Value
Cuvier’s	0.77	Mooring ID	1255.7	<0.001
		chl _a	57.89	<0.001
		SSH	28.93	<0.001
		sdSST	18.46	<0.01
		relSST	12.37	<0.05
Sowerby’s	0.70	Mooring ID	420.24	<0.001
		chl _a	99.23	<0.001
		SSH	26.98	<0.001
		relSST	23.1	<0.001
		sdSST	13.13	<0.05

For Sowerby’s beaked whales, all oceanographic covariates (chl_a, sdSST, relSST and SSH) were retained as smooth terms and the final selected model contained all variables investigated (chl_a, sdSST, relSST, SSH and mooring ID) (*p*-values in Table 4). The confusion matrix gave an AUC of 0.70 and an ability of the model to predict correctly 79% of the presences and 51% of the absences. For both species the most important variable was the mooring ID, revealing the importance of the location of the recorders (*p*-values in Table 4). For both Cuvier’s and Sowerby’s beaked whales, the lowest probabilities of detection were found at M9 (Figure 3). At M4 to M8, Cuvier’s beaked whale probabilities of detection were the highest, in comparison with the northernmost stations M1 and M2, where probabilities were the lowest after those at M9. At M3, probabilities of detection were lower than those at M4 to M8 but higher than those at M1 and M2. For Sowerby’s beaked whales, there was a clear north-to-south gradient in probabilities of detection, with a gradual decrease from M1 to M9.

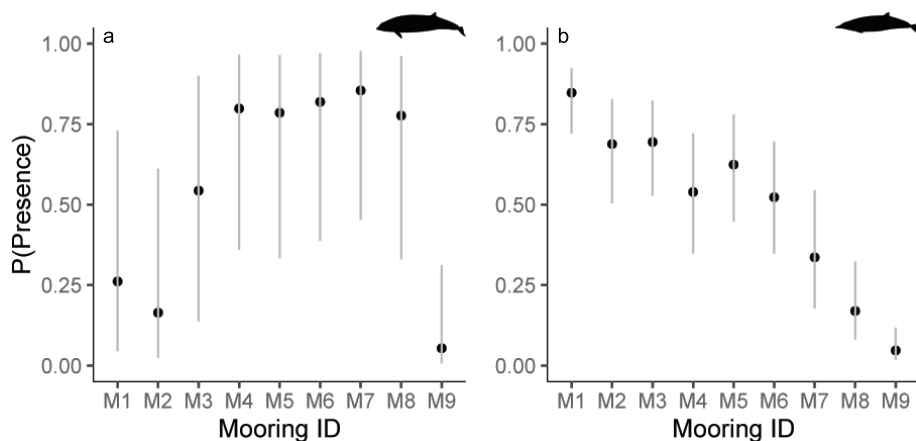


Figure 3. Probability of presence of (a) Cuvier’s and (b) Sowerby’s beaked whale clicks modelled as a function of the mooring ID. Shaded areas represent 95% confidence intervals.

The model results revealed that both Cuvier’s and Sowerby’s beaked whale clicks were overall less likely to be detected with increasing chl_a concentrations. This decrease was gradual throughout the range of chl_a for Sowerby’s beaked whales, but a brief increase in probability of detection was observed between a first gradual decrease and a final drop for Cuvier’s beaked whales (Figure 4). The modelled relationship between relSST and the presence of click detections was opposite for Cuvier’s and Sowerby’s beaked whales, with increasing probabilities of detection as relSST increased for the former and decreasing probabilities for the latter. For both species, probabilities of detection were relatively stable throughout the range of sdSST until a decrease occurred above values of approximately

0.30 °C. Finally, the probability of detecting both species increased overall as SSH values were increasing, so that it was the lowest when SSH values the most negative. However, the wide confidence intervals in some cases (especially for Cuvier’s beaked whales) suggested great caution should be taken in the interpretation of those observations.

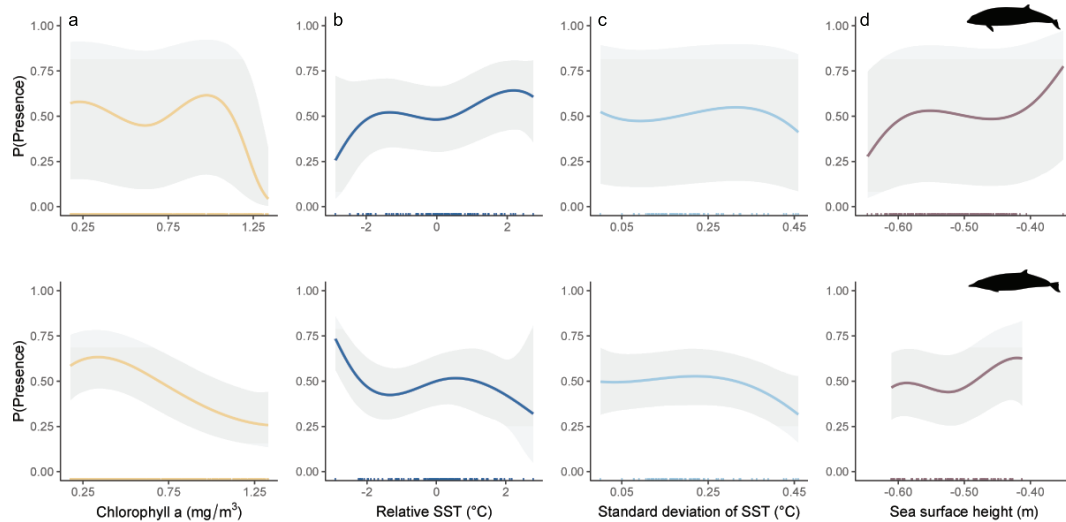


Figure 4. Probability of presence of Cuvier’s (first row) and Sowerby’s (second row) beaked whale clicks modelled as a smooth function of (a) chlorophyll a concentration, (b) relative sea surface temperature (SST), (c) standard deviation of SST and (d) sea surface height. Rug plots (on x–axes) indicate actual data values. Shaded areas represent 95% confidence intervals.

4. Discussion

This study combined acoustic data collected on an unprecedented scale in shelf-edge waters off western Ireland [63,64], an important area for several deep diving cetacean species. The exploitation of this large dataset already provided compelling evidence of the importance of the area for Cuvier’s and Sowerby’s beaked whales for the first time, highlighting their presence year-round [19,46,64]. To complement and build on those recent findings, we showed here the importance of oceanographic drivers for Cuvier’s and Sowerby’s beaked whales in this part of the northeast Atlantic. Specifically, chl a concentration, sdSST, relSST and SSH all significantly influenced the probability of click detection for both species. By including a variable to account for spatial variation in probabilities of detection, we also confirmed the latitudinal partitioning, different for each species, as showed by Kowarski et al. (2018) [46]. Specifically, Cuvier’s beaked whales seemed to be exploiting more southern locations along the continental shelf, while Sowerby’s preferred northern locations. The low probabilities of detection at M9 (not available in the latter study) also highlights the importance of the shelf edge in comparison with waters to the east of the Porcupine Seabight.

Various conditions known to enhance the local productivity have been described in the Irish Atlantic Margin and are likely to contribute to the aggregation of beaked whale prey. Interspersed with canyon and trough systems, the area is also subject to several currents, including the North Atlantic Current (NAC). The NAC creates large eddies in the Rockall Trough and generates currents to the west of the Porcupine shelf [65]. Deep tidal currents are present off the Porcupine Seabight and along slope regions [66]. The Shelf-Slope Front is the most important front feature in the area (running along the upper continental slope to the west of the Porcupine Bank) and is associated with the continuous Shelf Edge Current (SEC) [14]. Furthermore, upwelling cyclonic and downwelling anticyclonic eddies have been recorded along the Irish shelf break frontal zone [16,67]. If some seem to be temporary, lasting up to seven days [67], some persist for hundreds of days [16]. Associated with the

complex topography of the area, these oceanographic processes are likely to determine prey availability and in turn, the distribution and abundance of cetacean species [13,68].

Habitat modelling has the potential to inform management strategies by identifying environmental features influencing species distribution or abundance [8,43,69]. However, the most influential factor is likely to be prey distribution [70,71]. These data are often difficult to obtain, so environmental variables are often used as indicators of the actual forces driving predators' distribution [72,73]. Echolocation has been shown to be consistent during deep foraging dives in Cuvier's and Blainville's beaked whales [7] and can safely be assumed to be a crucial aspect of Sowerby's as well as other beaked whale species' foraging behaviour. Given the operating depth of the static recorders (average 1800 m), we can consider the detections in this study to be a proxy for Cuvier's and Sowerby's beaked whales' foraging activity, making the investigation of the influence of prey aggregating features particularly relevant.

Chlorophyll a concentration at the surface has been widely used as an indicator of primary productivity in studies focusing on deep-diving cetaceans [5,8,44,74,75]. Our results suggested a negative influence of chl a on Cuvier's and Sowerby's beaked whale foraging activity. Similar trends were reported by Correia et al. (2015) [74] but there is no general consensus in the literature, with either opposite effects [5] or no significant influence of chl a [8,75]. The challenge of collecting data on such elusive species is reflected in the literature, as many studies report on beaked whales as a functional group, rather than on individual species [8,74]. This could explain contradictory findings, as influences of chl a could vary across individual species.

We used metrics reflecting the occurrence of upwelling events (relSST) and frontal activity (sdSST) instead of absolute sea surface temperature. The results revealed that the highest probabilities of Sowerby's beaked whale click detections coincided with lower relSST values, which could indicate upwelling events. With Cuvier's however, detection rates seemed to generally increase with warmer relSST. Thermal fronts contribute to nutrient enhancement, affecting productivity and prey aggregation [51]. In several studies, they have been positively correlated with sperm whale aggregations [72,76,77], a species sharing a similar feeding ecology as beaked whales, targeting cephalopod species [78]. Here, Cuvier's and Sowerby's beaked whale detection rates were stable until sdSST values of approximately 0.30 °C, beyond which a negative relationship was observed. This subsequent decline in detection rates with increasing frontal activity was unexpected given the literature above but could be the result of a modelling artefact (e.g., influence of another factor unaccounted for) and might not have any ecological significance. Nonetheless, habitat modelling attempts on individual beaked whale species are scarce, which limited our ability to compare our findings.

The sea surface height was significant and moderately important in models for both species. The probability of detection of both Cuvier's and Sowerby's beaked whales was minimal when the SSH was the most negative. In the North Atlantic, SSH is generally depressed (i.e., negative values), which can reflect cyclonic eddies, associated with high productivity due to the occurrence of upwelling events [79]. Relationships between SSH and beaked whale presence have been reported previously, suggesting an association between the presence of the whales and that of eddies and upwelling phenomena [74,80]. In particular, Correia et al. (2015) [74] found that peaks in the presence of beaked whales corresponded with either high negative or high positive anomalies. However in our study, only negative SSH values were observed, which makes comparisons difficult.

The selection of variables for analysis must remain parsimonious and should be the result of a thorough reflection process and rely on an a priori knowledge on the area and the species of interest [43,81]. The nature of the data used should also be considered and justified the exclusion of topographic features in this study. The use of static recorders here allowed great temporal coverage but limited spatial coverage, which made topographical, static variables, uninformative, especially since similar habitats were monitored. Given the latitudinal range of deployment, untangling effects of the topography itself from effects

due to the latitude on beaked whale detection rates would not have been possible. Despite being more appropriate because of their temporal dynamism, the use of static recorders also limited the range of values from oceanographic variables. Complementary models would benefit from more extensive spatial coverage, to determine whether our results would be confirmed or whether different trends would emerge.

Determining the relevant scales to represent indirect prey-predator relationships is a central challenge in ecology [82]. The choice of which scales to investigate is however directly linked to the data exploited and with acoustic data, detection ranges should not exceed the scale of analysis [52]. In this study, the detection ranges were limited since beaked whale clicks attenuate quickly given their ultrasonic nature [11,12]. Sound propagation models in the area predicted detection ranges of 14 km and 4 km for Cuvier's and Sowerby's beaked whale clicks, respectively, [46,63,64]. By following a multi-scale approach [83,84], we have confirmed the importance of evaluating different spatio-temporal resolutions, with different variables being associated with beaked whale activity on different temporal and spatial scales. Although more strenuous, such a process is essential if one hopes to decipher the dynamism of species distribution in relation to a constantly changing environment [84]. We have found here that often, Cuvier's and Sowerby's beaked whales foraging activity was predominantly associated with features on different scales. Pinpointing the exact underlying ecological implications of these results is challenging but are likely to reflect differences in those species' ecology along the Irish Atlantic Margin. Recently, using the same dataset, Kowarski et al. (2018) [46] suggested the existence of a potential niche and latitudinal partitioning between those two beaked whale species, most likely linked to prey distribution, which we have confirmed here. Sowerby's prey on smaller cephalopods than Cuvier's beaked whales and fish is an important part of the diet of the former [78]. Differences in prey preferences, capture techniques or foraging strategies can therefore explain those findings.

This latitudinal partitioning could also be a confounding factor in the current study, by introducing some bias with regards to the influence of oceanographic features, given that all stations were pooled together. Furthermore, the fact that northern and southern stations were not sampled within the same calendar year further complexifies interpretations. Investigating site-by-site interactions could be revealing considering the topographical diversity in the area, but the lack of variability in oceanographic conditions at each station precluded such detailed analysis. Future investigations would most certainly benefit from added spatial variability in conditions, which could be obtained by exploiting transect data for example. However, even if acoustic methods are far more efficient to monitor such species than visual methods, instruments towed just below the surface do not come close to the capabilities of bottom-mounted devices in terms of beaked whale detection capabilities.

Overall, model performances were satisfactory but not optimal. For both species, the performance in capturing presences was good (over 79% for both species), but the model's ability to correctly classify absences was lower (60% and 51% for Cuvier's and Sowerby's, respectively). This is not surprising given the high detection rates throughout the area. Nonetheless, the approach undertaken here is most likely an oversimplification of the relationships between those whales and their environment, reinforced by potentially unknown missed predictors, which can also explain some of the results that do not align with the literature. Most of all, despite being relevant to represent factors influencing prey availability, proxies are not as reliable or as informative as direct prey data [44], given the important gap between physical processes and the top of the food chain, especially for species feeding at great depths. Direct information about prey stocks is very difficult to obtain, especially in challenging open seas and even more so when the species of interest is of low commercial value [78]. Furthermore, despite allowing a certain amount of flexibility, the use of remotely sensed data has limitations given that they only reflect surface conditions. The translation of processes occurring at the surface to those at greater depths is not clearly understood and sometimes controversial [51]. This is problematic when using data from bottom-mounted instruments, collected at great depths. Technological

advances offer alternative solutions such as Autonomous Underwater Vehicles equipped with multibeam sonar technologies, which can give valuable information on abundance and distribution of prey species [85]. In general, multidisciplinary, holistic approaches collecting data on both biotic and abiotic parameters simultaneously [86] are the way forward and root themselves in a more ambitious ecosystem-based management strategy [87]. Despite its limitations, this study gave an insight into the environmental preferences of Cuvier's and Sowerby's beaked whales, on which very little is known. This study will therefore serve as a point of reference for future investigations on habitat preferences for those species worldwide. It also highlights the value of static acoustic monitoring techniques for detecting those elusive species.

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Data Availability Statement: Restrictions apply to the availability of these data. Data for stations M1 to M8 are owned by the Irish Department of Communications, Climate Action and Environment and requests for access to the raw acoustic data can be submitted to PADadmin@DCCAE.gov.ie. Data for stations M9 are owned by Woodside Energy Ltd. (Perth, Australia) and the Galway-Mayo Institute of Technology.

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Abbreviations

The following abbreviations are used in this manuscript:

AMAR	Autonomous Multichannel Acoustic Recorders
AUC	Area Under the Curve
AVHRR	Advanced Very High Resolution Radiometer
chl _a	chlorophyll a
EU	European Union
GAM	Generalised Additive Model
GEE	Generalised Estimating Equation
GLM	Generalised Linear Model
MODIS	Moderate Resolution Imaging Spectroradiometer
MSFD	Marine Strategy Framework Directive
NAC	North Atlantic Current
PAM	Passive Acoustic Monitoring
POES	Polar Operational Environmental Satellites

QIC	Quasi-likelihood Independence model Criterion
relSST	relative sea surface temperature
ROC	Receiver Operating Characteristic
sdSST	standard deviation of sea surface temperature
SeaDAS	SeaWiFS Data Analysis System
SEC	Shelf Edge Current
SSH	Sea surface height

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