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Data Availability Statement: Beaked whale occurrence results from automated detectors and manual analysis are provided in spreadsheet form as Supporting Information. Therefore, all information necessary to replicate our study is available. The raw acoustic data cannot be made readily available due to size limitations (more than 17 TB). The acoustic data is owned by the Irish Department of Communications, Climate Action and Environment. The authors were given no special access privileges to the acoustic data and requests for access to the entirety of the raw

RESEARCH ARTICLE

Signals from the deep: Spatial and temporal acoustic occurrence of beaked whales off western Ireland

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Abstract

Little is known of the spatio-temporal occurrence of beaked whales off western Ireland, limiting the ability of Regulators to implement appropriate management and conservation measures. To address this knowledge gap, static acoustic monitoring was carried out using eight fixed bottom-mounted autonomous acoustic recorders: four from May to December 2015 on Ireland's northern slope and four from March to November 2016 on the western and southern slopes. Recorders ran for 205 to 230 days, resulting in 4.09 TB of data sampled at 250 kHz which could capture beaked whale acoustic signals. Zero-crossing-based automated detectors identified beaked whale clicks. A sample of detections was manually validated to evaluate and optimize detector performance. Analysis confirmed the occurrence of Sowerby's and Cuvier's beaked whales and Northern bottlenose whales. Northern bottlenose whale clicks occurred in late summer and autumn, but were too few to allow further analysis. Cuvier's and Sowerby's clicks occurred at all stations throughout the monitoring period. There was a significant effect of month and station (latitude) on the mean daily number of click detections for both species. Cuvier's clicks were more abundant at lower latitudes while Sowerby's were greater at higher latitudes, particularly in the spring, suggesting a spatial segregation between species, possibly driven by prey preference. Cuvier's occurrence increased in late autumn 2015 off northwest Porcupine Bank, a region of higher relative occurrence for each species. Seismic airgun shots, with daily sound exposure levels as high as 175 dB re 1 µPa²·s, did not appear to impact the mean daily number of Cuvier's or Sowerby's beaked whale click detections. This work provides insight into the significance of Irish waters for beaked whales and highlights the importance of using acoustics for beaked whale monitoring.

Introduction

The conservation and management of marine mammal populations is inherently constrained by the quantity and quality of available information on the ecology and distribution of the species of interest [1-3]. Collecting reliable data on some cetacean species that are highly mobile,



acoustic data from ObSERVE (in the same manner as the authors) can be submitted to PADadmin@DCCAE.gov.ie.

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Competing interests: Our affiliation with JASCO Applied Sciences does not alter our adherence to PLOS ONE policies on sharing data and materials.

deep-diving, wide ranging, and rare is particularly challenging. This problem could result in inadequate conservation measures [4, 5] or a lack of compliance with international directives [6]. Such issues are particularly topical for species belonging to the Ziphiidae family, known as beaked whales.

Beaked whales are among the most diverse but least known cetaceans globally, with comparatively little information available on their distribution, ecology and population structure [7, 8]. They occur worldwide, typically in offshore pelagic habitats where they show a preference for continental slope waters, deep ocean troughs, and canyons [9-11]. Their deep oceanic habitat and elusive behaviour including long, deep dives followed by short surface intervals have made these species difficult to study using traditional line-transect methods that are constrained by weather conditions [2, 4]. Ziphiid movements and distribution are likely driven by that of their prey. For example, Giorli et al. [12] hypothesized that Ziphiids move between areas to optimize their access to prey in Hawaii. Indeed, beaked whale foraging behaviour differs across species, oceans, habitats, time of day, and season [2, 12-15]. Globally, beaked whales are considered Data Deficient, except for the Cuvier's beaked whale (Ziphius cavirostris) and Southern bottlenose whale (Hyperoodon planifrons) which have been categorized as species of Least Concern [16]. Observations and research in recent decades has shown beaked whales to be sensitive to several human maritime activities, particularly the use of mid-frequency military sonar which has been linked to behavioural changes, temporary area avoidance, and fatal mass stranding events [17-26]. It has further been shown that shipping may affect beaked whale diving and foraging behaviour and intense sound sources from seismic surveys are also of concern [27]. Even small changes in the dive cycle of beaked whales, caused by anthropogenic disturbance, could cause decompression sickness since long dive times result in relatively high nitrogen concentration in their tissues [27-30], though such an acute outcome was not observed during controlled exposure studies (e.g. [24, 31, 32]). As information on beaked whale responses to human activities in the ocean grows, it is increasingly necessary to improve our baseline understanding of their distribution, habitat use and ecology [2].

Ireland's Exclusive Economic Zone holds significant energy resources that are expected to contribute to the development of the Irish economy and to Ireland's energy security. Nearshore areas are currently being investigated for wave, wind, and tidal energy installations. The western part of the Irish continental shelf and down the continental slope, an area known as the Atlantic Margin, is thought to offer considerable potential reserves of oil and gas. The Atlantic Margin's continental slope is topographically diverse, being cut by several troughs and canyons, and it has been described as one of the more biologically productive regions of the North-East Atlantic, making it potentially suitable habitat for many cetaceans, including Ziphiids [6, 33, 34].

Five beaked whale species have been reported in Irish waters thus far. Cuvier's beaked whales were observed during surveys that included the Atlantic Margin [4, 33, 35–38]. This species is the most frequently stranded beaked whale in Ireland, leaving some to speculate that Cuvier's may breed in the region [3, 34]. Northern bottlenose whales (*Hyperoodon ampullatus*) have stranded on 50 occasions [3, 39] and have been infrequently sighted [4, 33, 38]. Sowerby's beaked whales (*Mesoplodon bidens*) have occasionally been observed offshore [4, 33, 38] and the few strandings have not shown any seasonality [3]. There has only been one sighting thought to be True's beaked whale (*Mesoplodon mirus*) along the Atlantic Margin [33]. Finally, Gervais' beaked whales (*Mesoplodon europaeus*) are known in Ireland from a single stranding [40]. In the UK, Blainville's beaked whales (*M. densirostris*) have stranded on two occasions [41–43] and therefore may also occur in Irish waters. Offshore Atlantic surveys in effective weather conditions have largely been limited to summer months with all studies concluding that research on a wider spatio-temporal scale is required to understand the distribution and movements of these cryptic animals [4, 6, 33, 38].



All cetacean species in Irish waters are protected under national and international legislation [44, 45]. To effectively achieve this mandate, knowledge gaps regarding the spatial and temporal use of areas of interest for oil and gas exploration or other industrial practices by marine mammals must be investigated and addressed. In this regard, a comprehensive acoustic project, ObSERVE Acoustic, was conceived and commissioned by Ireland's Department of Communications, Climate Action and Environment, and the Department of Culture, Heritage and the Gaeltacht to provide robust data with which to inform conservation and management in the Atlantic Margin by assessing the importance of these shelf edge habitats for beaked whales and other cetaceans.

We used passive acoustic monitoring (PAM) techniques to monitor for Ziphiids on an unprecedented scale. Smaller scale PAM projects have previously successfully recorded beaked whale acoustics in the area [46, 47], but were rarely able to confidently identify the species concerned. As a monitoring technique, PAM offers several benefits over conventional visual survey methods. For example, data can be collected continuously in a cost-effective manner in deep, offshore, remote waters regardless of light and weather conditions. Detection of cetaceans is, however, dependent on their sound production. Marine mammals rely on sound for many vital functions including navigation, foraging, and breeding [48, 49]. Although the acoustic signals of many beaked whale species remain unknown or poorly described, among North Atlantic species the clicks of Northern Bottlenose whale [50–52], Cuvier's [53, 54], Sowerby's [55], and Gervais' beaked whales [53, 56] have been described. Notably, the click characteristics are unique for each species which allows for reliable acoustic identification. In this study, we assessed the spatial and temporal distribution of acoustically active beaked whale species in the Atlantic Margin over the course of two years using static acoustic recorders.

Methods

Data collection

Acoustic data were collected using Autonomous Multichannel Acoustic Recorders (AMARs; JASCO Applied Sciences) suspended approximately 15 m above the seafloor at four locations in 2015 (stations 1–4) and at five locations in 2016 (stations 3 and 5–8; Fig 1 and Table 1).

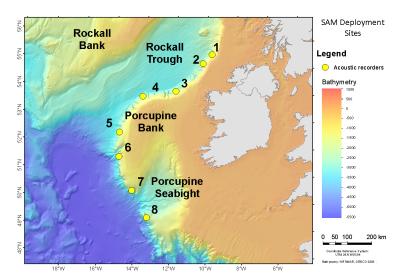


Fig 1. Acoustic monitoring stations using AMARs in the Atlantic Margin study area off western Ireland during 2015 (stations 1-4) and 2016 (stations 3 and 5-8).



Table 1. The location, depth, and operation period of AMARs deployed off western Ireland at eight stations.

Station	Latitude (°N)	Longitude (°W)	Depth (m)	Start day	End day	Year	Total no. of recording days
1	55.6302	-9.7302	1600	08 May	22 Aug	2015	214
	55.6323	-9.7252	1620	29 Aug	13 Dec	2015	
2	55.3018	-10.3084	1995	08 May	22 Aug	2015	214
	55.3011	-10.3037	1971	29 Aug	13 Dec	2015	
3	54.2513	-11.9940	1850	30 Aug	14 Dec	2015	205
	54.2502	-11.9926	1770	24 Mar	29 Jun	2016	
4	54.0014	-14.0424	1920	07 May	20 Aug	2015	213
	54.0015	-14.0429	1944	30 Aug	14 Dec	2015	
5	52.6225	-15.3045	1752	21 Mar	10 Jul	2016	227
	52.6221	-15.3046	1750	10 Jul	02 Nov	2016	
6	51.7226	-15.2077	1765	20 Mar	11 Jul	2016	210
	51.7245	-15.2342	1745	11 Jul	15 Oct	2016	
7	50.5096	-14.3124	1750	19 Mar	11 Jul	2016	230
	50.5085	-14.3150	1750	11 Jul	03 Nov	2016	
8	49.5477	-13.3730	1760	19 Mar	9 Aug	2016	230
	49.5478	-13.3723	1760	09 Aug	03 Nov	2016	

Data collection occurred over four recording periods: May to Aug 2015, Aug to Dec 2015, Mar to July/Aug 2016, and Jul/Aug to Oct/Nov 2016 (Table 1). In 2015, each AMAR was fitted with an HTI–99-HF omnidirectional hydrophone (High Tech Inc., -164 dB re 1 V/ μ Pa sensitivity). In 2016, M36-V35-100 omnidirectional hydrophones (GeoSpectrum, -165 dB re 1 V/ μ Pa sensitivity) were used. Recorders sampled on 8 min duty cycles in 2015 and 14.5 to 15 min duty cycles in 2016 (Table 2). Low sampling rates (32 and 2 kHz) were used to record lower frequency marine mammal vocalizations. The low frequency channels had 24-bit resolution with a spectral noise floor of 29 dB re 1 μ Pa²/Hz and a nominal ceiling of 165 dB re 1 μ Pa. High sampling rate (250 kHz) channels were used to record high frequency odontocete clicks, including those of beaked whales that are described here. The high frequency channels had 16-bit resolution with a spectral noise floor of 35 dB re 1 μ Pa²/Hz and a nominal ceiling of 171 dB re 1 μ Pa. Acoustic data were stored on internal solid-state flash memory for post-retrieval processing. Instrument retrieval was achieved via an acoustic release.

Table 2. The duty cycle, including duration at each sampling rate, of AMARs deployed in May—Dec of 2015, March—Jul of 2016, and July—Nov of 2016.

Deployment timeframe	Duty Cycle (min)	Sampling rate (kHz)	Duration (sec)	
May-Dec 2015	8	32	342	
		250	130	
		sleep	8	
Mar-Jul 2016	14.5	2	678	
		250	95	
		sleep	90	
Jul-Nov 2016	15	32	680	
		250	97	
		sleep	90	

The 32 and 2 kHz sampling rate channels had 24-bit resolution with a spectral noise floor of 29 dB re 1 μ Pa 2 /Hz and a nominal ceiling of 165 dB re 1 μ Pa. The 250 kHz sampling rate channels had 16-bit resolution with a spectral noise floor of 35 dB re 1 μ Pa 2 /Hz and a nominal ceiling of 171 dB re 1 μ Pa.



Automatic detection

Odontocete clicks were identified using JASCO's custom combined energy-detector and classification algorithm. The software used a Teager-Kaiser energy detector to identify potential clicks in the data and then computed three zero-crossing features of each click: the number of zero-crossings, the median time between zero-crossings, and the median change in time between zero-crossings. These features were compared to an acoustic library of odontocete clicks known to be from beaked whales and each click was classified as the species with the lowest Mahalanobis distance from equivalent library template parameters. From here on, the combined detector-classifier is referred to as the detector or the automated detector and its outputs are called detections.

To determine automated detector performance and verify species occurrence, a selection of acoustic files was visually and aurally reviewed by experienced bio-acoustic analysts using PAMlab (JASCO Applied Sciences). Files selected for manual review were distributed across time of year, time of day, the number of automated detections, and the number of species automatically detected (both beaked whales and other odontocetes). The presence or absence of identifiable signals of every beaked whale species, as well as any other sounds of interest including seismic impulses and naval sonar, was noted for every file reviewed. Beaked whale species were identified based on species-specific click characteristics previously described in the literature [2, 50-56]. Note that the validation process characterizes the ability of the automated detector to identify at least one click in each file and does not discern between files in which all clicks were correctly identified and those in which only a portion of clicks was correctly identified. It does not characterize the performance of the automated detector in identifying individual clicks. This method allowed us to calculate the automated detector performance. We captured the frequency at which automated detectors missed calls (false negatives; FN), correctly identified them (true positives; TP), and incorrectly identified them (false positive; FP) on a 'per acoustic file' basis. To optimize our results, we utilized a maximum likelihood estimator that compared manual and automated results to determine the minimum number of automated detections per acoustic file, i.e. the detection threshold, that maximized the "F-score" [57]:

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

where the automated detector's precision (P) is the proportion of detections that are accurate, and recall (R) is the proportion of recorded beaked whale clicks that are automatically detected on a per file basis [58, 59]. To maximize the reliability of our results, a greater emphasis was placed on precision than recall ($\beta = 0.5$).

One-min sound files in which the automated detections met or exceeded the minimum detection threshold are presented as species presence/absence per acoustic file in daily and hourly occurrence plots. The mean number of automated detections per day are presented by station and month excluding detections in any acoustic files where the minimum detection threshold was not met. Although the acoustic data at stations 1–4 and 5–8 were recorded in 2015 and 2016, respectively, they are displayed on the same monthly time scale for ease of reading and interpretation.

During manual validation of beaked whale presence, seismic impulses were observed. Therefore, JASCO's seismic pulse sequence detector [60] was used to identify periods with seismic survey pulses. The software detects energy within pre-defined time frequency bins that is at least three times greater than the median value and then joins adjacent bins thereby creating contours. Contours 0.2–6-seconds in duration with a bandwidth of at least 60 Hz are



retained. The software algorithm looks for repeating retained contour events with spacings of 4.8 – 65s, the normal range of seismic pulse periods. Where at least six regularly spaced contours occur, the automated detector signals the occurrence of a seismic pulse sequence. Results from the seismic pulse sequence detector were compared to seismic survey events noted during manual validation of beaked whale clicks and these were found to accurately reflect seismic occurrence.

Statistical analysis

Statistical analysis was carried out for each beaked whale species detected with high accuracy (F-score > 0.80). First, a multivariate analysis of variance (MANOVA) tested for the difference in the number of mean daily detections across months, stations, and days where seismic signals were present versus absent. Parameters identified by the MANOVA as significant were further explored. The null hypothesis that the mean number of detections per day of each species was constant across the eight stations was tested with non-parametric Kruskal-Wallis tests [61]. Where the null hypothesis was rejected, a Tukey-Kramer multiple comparison test allowed us to determine which stations differed. The same statistical techniques were implemented to test the null hypothesis that, for each species, the mean number of detections per recording day was constant across recording months.

Diel patterns were explored using all days with detections across every station. For every day, each hour containing detections (detection hour) was categorized as occurring in one of four light periods based on nautical time: dawn (sun is 12° below horizon to sunrise), light (sunrise to sunset), dusk (sunset to when the sun is below the horizon by 12°), and dark (sun is less than 12° below the horizon). Sunset, sunrise, nautical dusk, and nautical dawn times were acquired from [62]. For every day, the number of detection hours in each light period was divided by the total hours in the associated light period to produce the average detection hours per light period. In this manner, detection occurrence was normalized and the variability in daily light periods over the course of the study was accounted for. To address the daily variation in the number of detection hours, the mean detection hours of each day was subtracted from the average detection hours per light period, resulting in the mean adjusted detection hours. Welch's ANOVA was used to test the null hypothesis that the mean adjusted detection hours were constant across diel light periods [61]. A Tukey-Kramer multiple comparison test determined if the mean-adjusted hours with detections differed significantly between any diel light periods [63, 64].

Results

Static acoustic monitoring resulted in 1656.8 days (19.26 TB) of acoustics data, of which 4.09 TB had a sampling rate of 250 kHz and was thus suitable for beaked whale occurrence analysis.

Beaked whale detector performance

A manual review of 2,530 acoustic files (1.07% of recordings or 74.3 hours of data) sampled at 250 kHz confirmed the presence of beaked whales in 780 acoustic files. Cuvier's and Sowerby's beaked whales and northern bottlenose whale clicks were observed (Fig 2). Clicks attributed to Cuvier's beaked whales and northern bottlenose whales were based on previous descriptions of these species by Zimmer et al. [54] and Martin et al. [52], respectively. The click type denoted as Sowerby's beaked whale is similar in frequency characteristics to the high frequency Sowerby's beaked whale click described from surface recordings by Cholewiak et al. [55] and it matches the click type identified as Sowerby's beaked whale by Stanistreet et al. [2]. We did not observe clicks matching any of the lower frequency Sowerby's beaked whale click types



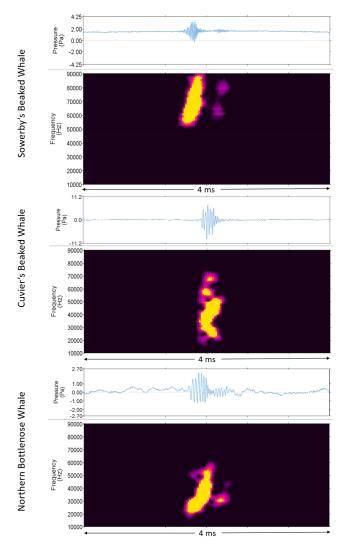


Fig 2. Waveform (top) and spectrogram (bottom) of beaked whale clicks. A Sowerby's beaked whale click recorded at station 1 on 5 Sept 2015 at 14:26, a Cuvier's beaked whale click recorded at station 3 on 29 Nov 2015 at 17:56, and a northern bottlenose whale click recorded at station 1 on 12 Sept 2015 at 20:10 (right; 512 Hz frequency resolution, 2.6 ms time window, 0.2 ms time step, Hamming window).

described by Cholewiak et al. [55], potentially reflecting a difference between surface versus deep diving (foraging) click behaviour.

The Cuvier's beaked whale click classifier had a precision of 0.87 and recall of 0.79 (F-score = 0.86, Table 3). The Sowerby's beaked whale click classifier performed similarly well, capturing 93% of acoustic files where Sowerby's occurred, of which 96% truly contained

Table 3. Automated detector precision (P), recall (R), and F-score (F) prior (original) and after (optimized) application of detection thresholds for the beaked whale species detected off western Ireland on static acoustic recorders in 2015 and 2016.

Species	P ^{Original}	R ^{Original}	F ^{Original}	Threshold	P ^{Optimized}	R ^{Optimized}	F ^{Optimized}
Cuvier's	0.87	0.79	0.86	1	0.87	0.79	0.86
Sowerby's	0.96	0.93	0.95	1	0.96	0.93	0.95
Northern bottlenose	0.11	0.79	0.13	15	1.00	0.42	0.78

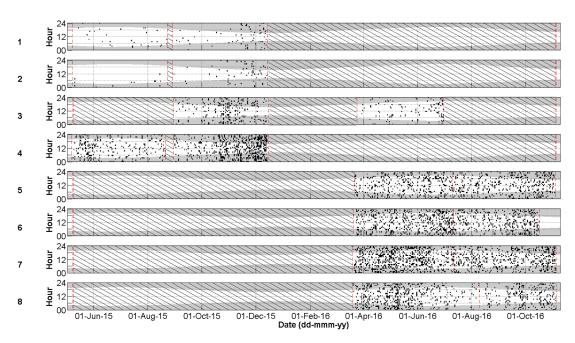


Fig 3. Daily and hourly occurrence of Cuvier's beaked whale clicks per acoustic file at stations 1-8 represented as individual black dots (P=0.87, R=0.79). Shaded areas indicate periods of darkness. The red dashed lines indicate the deployment and retrieval dates. Black diagonal lines indicate periods with no data.

Sowerby's beaked whale clicks (F-score = 0.95, Table 3). The northern bottlenose whale click classifier required optimization via implementation of a detector threshold. Acoustic files with less than 15 detections were not included resulting in a precision of 1.00, though only 42% of acoustic files where northern bottlenose signals occurred were captured (F-score = 0.78, Table 3).

Cuvier's beaked whales

Cuvier's beaked whale clicks occurred throughout the recording period at all stations with the species present on 72.8% of recording days (Fig 3 and Table 4). MANOVA results indicate that the mean daily number of Cuvier's beaked whale detections was significantly different between monitoring stations and between months of the year (Table 5). Indeed, station 4, at the northern edge of Porcupine Bank, had the highest mean daily Cuvier's detections while the lowest mean detections per day were observed at the northernmost stations 1 and 2 (Fig 4). Intermediate detection rates occurred at stations 3 and 5 to 8 (Fig 4). In 2015, when stations

Table 4. Percentage of days with Cuvier's beaked, Sowerby's beaked, and northern bottlenose whale clicks recorded at 8 stations off western Ireland in 2015 and 2016.

Station	Cuvier's beaked whale	Sowerby's beaked whale	Northern bottlenose whale
1	30.4	84.1	0.5
2	20.6	57.0	0.0
3	63.9	75.6	0.5
4	87.3	75.1	2.8
5	93.8	69.2	0.9
6	97.1	53.8	0.5
7	98.3	38.3	0.0
8	87.0	18.7	0.0



Table 5	Results	of Cuvie	r's MA	NOVA

Variable(s)	Sum of Squares	df	F-value	P-value
Month	2.43x10 ⁵	16	25.5	< 0.001
Station	3.06x10 ⁵	7	73.3	< 0.001
Seismic	118	1	0.20	0.66
Month, Station	2.68x10 ⁵	44	10.2	< 0.001
Month, Seismic	$3.46x10^3$	12	0.48	0.93
Station, Seismic	1.33 x10 ³	4	0.56	0.69
Month, Station, Seismic	909	4	0.38	0.82

Includes the sum of squares, degrees of freedom (df), F-value, and P-value where the response variable was the mean number of Cuvier's beaked whale detections per day and the statistical significance level was <0.05.

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were in the northern half of the study area, the mean daily detections were higher on average in the months of October, November, and December than from May to September (Fig 5); a pattern driven by the high number of detections at station 4 in the winter of 2015. December 2015 had more detections than any other month of that year (Fig 5). In contrast, in 2016 when stations were deployed further south, Cuvier's beaked whale mean daily detections increased through the spring, decreased in the summer, and increased again in the autumn (Fig 5). However, these trends were not statistically significant (Fig 5).

The adjusted mean hours with Cuvier's beaked whale clicks were highest during dark $(4.7 \times 10^{-3}; SE = 3.9 \times 10^{-3})$ and lowest during light $(-4.4 \times 10^{-3}; SE = 4.1 \times 10^{-3})$ with dawn and dusk values intermediate at 0.005 (SE = 8.4×10^{-3}) and 1.8×10^{-4} (SE = 8.1×10^{-3}), respectively (Fig 6). All light periods had a sample size (n) of 1270. The null hypothesis that the medians of the mean hours with Cuvier's beaked whale clicks did not differ between the four light periods was not rejected by Welch's ANOVA (Fig 6).

Sowerby's beaked whales

Sowerby's beaked whale clicks were present at all stations in 2015 and 2016, occurring on 58.4% of recording days (Fig 7 and Table 4). Like Cuvier's beaked whales, Sowerby's beaked

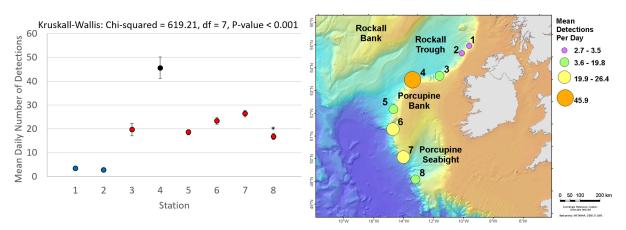


Fig 4. Mean Cuvier's beaked whale detections per recording day bubble plot (right) and with standard error bars (left) for stations 1 (SE = ± 0.70), 2 (SE = ± 0.59), 3 (SE = ± 2.61), 4 (SE = ± 4.48), 5 (SE = ± 1.08), 6 (SE = ± 1.38), 7 (SE = ± 1.35), and 8 (SE = ± 1.26) off western Ireland from May to Dec 2015 (stations 1–4) and Mar to Nov 2016 (stations 3 and 5–8). Results of Kruskall-Wallis tests are given and results from Tukey-Kramer multiple comparisons tests are represented by coloured means (left) with different colours denoting a statistically significant difference. *Station 8 differs from 7, but not from 3, 5, and 6.



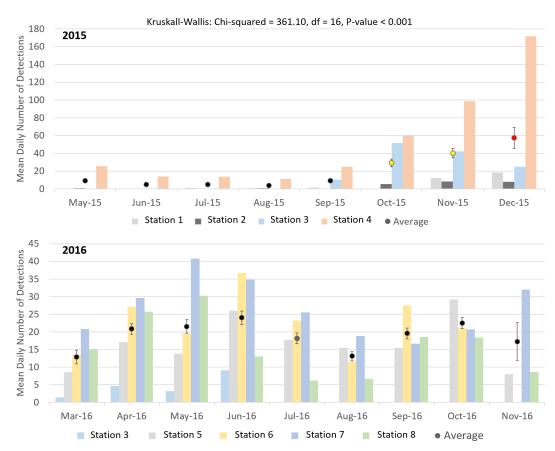


Fig 5. Mean daily number of Cuvier's beaked whale detections per month for each station that recorded data in 2015 (top) and 2016 (bottom), as well as the average across all stations with standard error bars. Results of Kruskall-Wallis tests are given and results from Tukey-Kramer multiple comparisons tests (applied to averages from 2015 and 2016 separately) are represented by coloured means with different colours denoting statistically significant differences.

whale clicks showed spatio-temporal variation with the mean number of detections per day being significantly different between months of the year and between stations (Table 6). The northernmost station 1 had significantly higher mean daily Sowerby's beaked whale detections than all other stations while station 8 had fewer detections than all stations but 7 (Fig 8). Station 4 has more detections than stations 2, 6, 7 and 8 (Fig 8). In 2015 when the four northern stations were monitored, the mean daily detections were highest on average in May, a pattern largely driven by the high number of detections at station 1 (Fig 9). November had significantly more detections than July, September, and October, with the detection rate in October also being significantly lower than August (Fig 9). On average in 2016 when the southern stations were monitored, there was no significant difference in the number of Sowerby's beaked whale detections between months (Fig 9).

The mean adjusted average hours with Sowerby's beaked whale clicks were highest during dark $(8.8 \times 10^{-3}; SE = 4.7 \times 10^{-3})$ and lowest during dawn $(-0.01; SE = 6.5 \times 10^{-3})$ and dusk $(-0.02; SE = 6.4 \times 10^{-3})$ with light intermediate at 3.5×10^{-3} ($SE = 1.9 \times 10^{-3}; Fig.6$). All light periods had a sample size (n) of 1019. The null hypothesis that the medians of the mean adjusted hours with Sowerby's beaked whale clicks did not differ between the four light periods was rejected (Fig.6). The mean adjusted hours with Sowerby's clicks during dark was significantly higher than during dawn and dusk, but no different than light. No significant difference in the means was observed between dawn, dusk, or light (Fig.6).



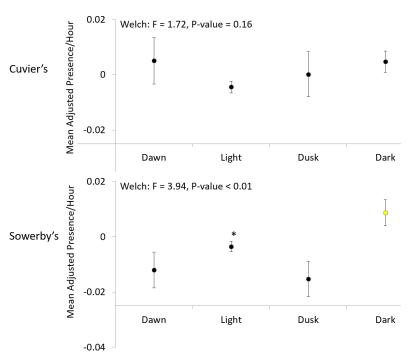


Fig 6. Mean adjusted hours with Cuvier's (top) and Sowerby's (bottom) beaked whale clicks with standard error bars in four light periods: dawn, light, dusk, and dark. Light period times were obtained from *Reda and Andreas (62)*. Results of Welch's ANOVA are given for each species and results from Tukey-Kramer multiple comparisons tests are represented by coloured means with different colours denoting statistically significant differences. *The Sowerby's light period does not differ significantly from any of the other light periods.

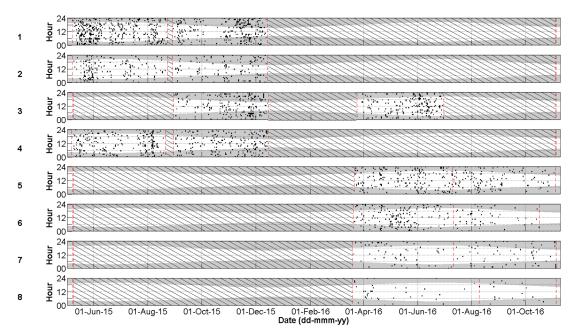


Fig 7. Daily and hourly occurrence of Sowerby's beaked whale clicks per acoustic file at stations 1-8 represented as individual black dots (P=0.96, R=0.93). Shaded areas indicate periods of darkness. The red dashed lines indicate the deployment and retrieval dates. Black diagonal lines indicate periods with no data.



Variable(s)	Sum of Squares	df	F-value	P-value
Month	$1.36 \text{x} 10^4$	16	10.4	< 0.001
Station	1.60x10 ⁴	7	27.8	< 0.001
Seismic	152	1	1.85	0.17
Month, Station	$1.01 \mathrm{x} 10^4$	44	2.79	< 0.001
Month, Seismic	878	10	1.07	0.38
Station, Seismic	$1.04 \mathrm{x} 10^3$	6	2.10	0.05
Month, Station, Seismic	960	17	0.69	0.82

Includes the sum of squares, degrees of freedom (df), F-value, and P-value where the response variable was the mean number of Sowerby's beaked whale detections per day and the statistical significance level was <0.05.

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Northern bottlenose whales

Northern bottlenose whale clicks were rare, only occurring in the summer and autumn on 1.0% of recording days (Fig 10 and Table 4). In 2015 clicks were recorded on 19, 26, 29, 31 Jul, 16 Aug, and 2 Sept at station 4, 4 Sept at station 3 and on 12 Sept at station 1. In 2016 northern bottlenose whale clicks occurred at station 5 on 26 Aug and 13 Sept and at station 6 on 30 Aug. They were never automatically or manually detected at stations 2, 7, or 8 and were absent in the acoustic dataset from the months of April to June and from October to December.

Seismic impulses

Seismic impulse detections occurred at all stations in 2015 and 2016 almost exclusively from June to October, but were most prominent at the more southerly stations 7 and 8 (Fig 11). Indeed, from 1 June to 1 October, seismic impulse detections occurred on 49.4% of recording days (Fig 11; 19.1% at station 1, 20.0% at station 2, 16.7% at station 3, 30.4% at station 4, 76.2% at station 5, 45.9% at station 6, 82.8% at station 7, and 82.8% at station 8). Seismic survey pulses occurred in bouts with gaps of up to a few days duration. MANOVA results indicate that the mean number of acoustic files with Cuvier's beaked whale clicks were not significantly different between days when seismic was present against days when seismic was absent (Table 5).

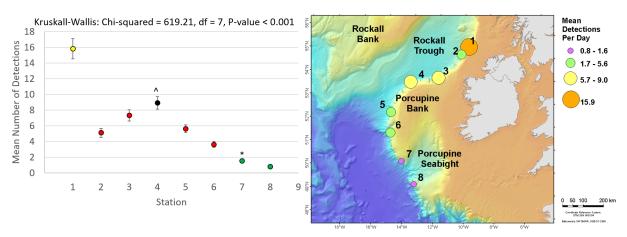


Fig 8. Mean Sowerby's beaked whale detections per recording day bubble plot (right) and with standard error bars (left) for stations 1 (SE = ± 1.28), 2 (SE = ± 0.56), 3 (SE = ± 0.70), 4 (SE = ± 0.87), 5 (SE = ± 0.87), 6 (SE = ± 0.87), 7 (SE = ± 0.23), and 8 (SE = ± 0.15) off western Ireland from May to Dec 2015 (stations 1–4) and Mar to Nov 2016 (stations 3 and 5–8). Results of Kruskall-Wallis tests are given and results from Tukey-Kramer multiple comparisons tests are represented by coloured means (left) with different colours denoting statistically significant differences. Astation 4 does not differ from 3 or 5. *Station 7 does not differ from 8 or 6, but 8 differs from 6.



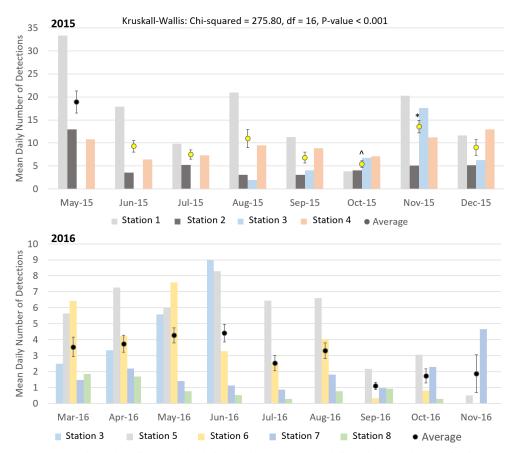


Fig 9. Mean daily number of Sowerby's beaked whale detections per month for each station that recorded data in 2015 (top) and 2016 (bottom) as well as the average across all stations with standard error bars. Results of Kruskall-Wallis tests are given and results from Tukey-Kramer multiple comparisons tests (applied to average of 2015 and 2016 separately) are represented by coloured means with different colours denoting statistically significant differences.

*November 2015 differs from July and October 2015, but not from June, August, September, or December 2015.

^October 2015 differs from August 2015.

Nor was there a significant difference between the mean number of acoustic files with Sowerby's clicks when seismic was present versus absent (Table 6).

Station 8 had the highest level of seismic activity (Fig 11). The daily sound exposure levels were calculated for station 8, both unweighted and using the marine-mammal auditory weighting functions suggested in [65] (Fig 12). The unweighted sound exposures increased from the range of 154–163 dB re 1 μ Pa²·s before seismic started to 165–175 dB re 1 μ Pa²·s when seismic was present. Most of the seismic energy was in the lowest frequency bands and did not increase the daily sound exposure level when the sound was weighted for the mid and high frequency cetacean groups, which includes the beaked whales. The sound exposure levels never approached the thresholds for possible temporary auditory injury to any of the marine mammal groups [66].

Discussion

Three beaked whale species were acoustically present in the northern Atlantic Margin off western Ireland in 2015 and in the southern Atlantic Margin in 2016. During both monitoring periods, Cuvier's and Sowerby's beaked whale clicks were common while northern bottlenose whale clicks were rare. Although the interpretation of spatial and temporal acoustic occurrence



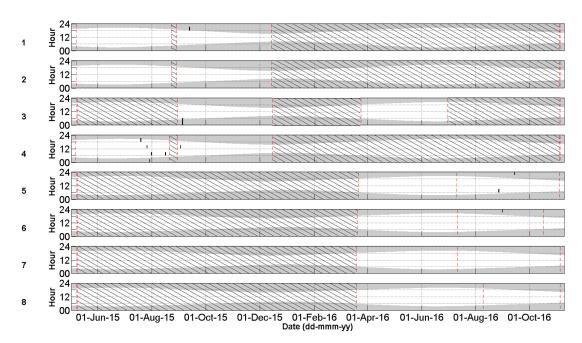


Fig 10. Daily and hourly occurrence of northern bottlenose whale clicks per acoustic file at stations 1–8 represented as individual black dots (P = 1, R = 0.42). Shaded areas indicate periods of darkness. The red dashed lines indicate the deployment and retrieval dates. Black diagonal lines indicate periods with no data.

patterns presented here is somewhat obscured by the fact that the whole area was not sampled within the same calendar year and winter months were not sampled beyond early to mid-December 2015 and early November 2016, this study provides valuable new data in space and time regarding beaked whale occurrence in this part of the North-East Atlantic. It also

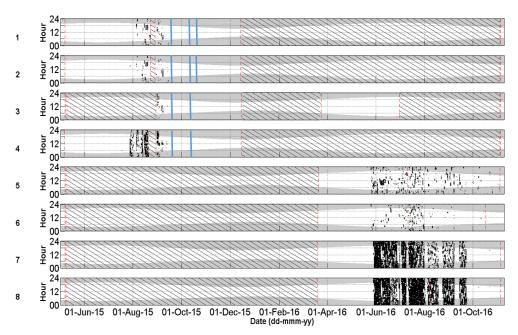


Fig 11. Daily and hourly occurrence of seismic impulses (black dots) at stations 1–8. Shaded areas indicate periods of darkness. The red dashed lines indicate the deployment and retrieval dates. Black diagonal lines indicate periods with no data. Blue solid lines indicate days when sonar was opportunistically observed.



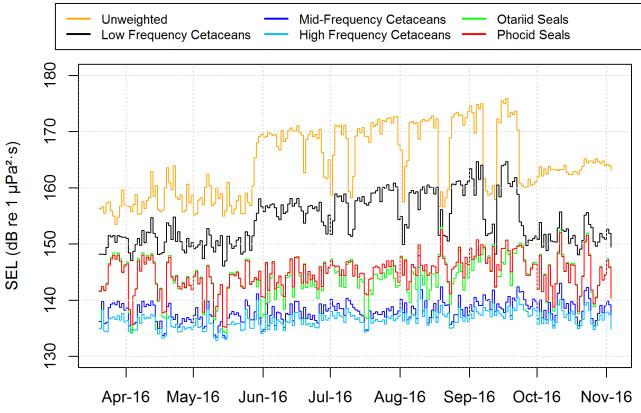


Fig 12. Daily unweighted and marine-mammal auditory filter weighted [66] sound exposure levels for station 8 which had the highest seismic sound levels across all eight deployments.

provides the first insights into the importance of the Atlantic Margin for Cuvier's and Sowerby's beaked whales and establishes a baseline for beaked whale monitoring and assessment off western Ireland.

The static acoustic recorders had a limited beaked whale detection range since Ziphiid acoustic signals are high frequency in nature and thus attenuate quickly with distance in the water column, even in ideal acoustic conditions. For example, it is predicted that most Ziphiids cannot be detected beyond 4 km [67], although Blainville's beaked whales have been detected up to 6.5 km in the Bahamas [68]. Sound propagation modeling within the Porcupine Seabight off southwest Ireland predicted that Cuvier's and Sowerby's beaked whales cannot be detected beyond 14 km and 4 km, respectively (Sam Denes, personal communication). Northern bottlenose whales have an estimated detectability radius of up to 8 km in a submarine canyon off eastern Canada (Sam Denes, personal communication). Therefore, the beaked whales detected in the present study were certainly within 14 km of the recording stations, and more likely within 4 to 5 km most of the time. We can be confident that acoustic signals recorded at a station were not simultaneously recorded by others since the nearest stations (stations 1 and 2) were situated over 50 km apart. Due to the high beaked whale click frequencies, no seasonal differences in detection range due, to increased background noise in winter, for example, are expected [69].

Cuvier's beaked whales are one of the most widespread and abundant beaked whale species globally. In Ireland, they have the largest latitudinal range and are the most frequently stranded Ziphiid [3, 9, 70]. Although their presence in the Atlantic Margin region was expected, the



breadth and regularity of their occurrence were novel and somewhat unexpected given the limited sightings and acoustic detections during previous vessel-based visual and towed array surveys [3, 33, 38, 71]. Indeed, in a previous offshore study, O'Cadhla et al. [33] described only three sightings of this species: two in the Rockall Trough in August 2000 and one along the southern slope of the Porcupine Bank in August 2001. In a parallel towed acoustic study, Aguilar de Soto et al. [38] reported only a few Cuvier's beaked whale detections along the Atlantic Margin. Furthermore, an extensive northeast Atlantic visual survey found Cuvier's beaked whales to occur almost exclusively in the Bay of Biscay [4] to the south of our study area. The conflicting results between study methods highlight the necessity of utilizing PAM when studying such elusive animals.

Keeping in mind the caveats caused by the asynchronous sampling of northern and southern areas, Cuvier's beaked whales seemed to show a preference for more southern stations along the continental shelf edge from the northern slope of the Porcupine Bank to the southern entrance of the Porcupine Seabight, a pattern likely linked to their prey distribution. In European waters, the diet of Cuvier's beaked whale is dominated by cephalopods including Teuthowenia megalops, Taonius pavo, Histioteuthis reversa, Mastigoteuthis, Gonatus, and Chiroteuthis species [72-74]. Teuthowenia megalops is abundant and widely distributed in deep waters of the North Atlantic [75] and was the most abundant species of Cranchiid squid caught off Ireland by Collins et al. [76]. Histioteuthis reversa is a pelagic species found in the North Atlantic from 11° to 59°N and has been recorded in water depths of 1343-1794 m [77, 78]. These squid are thought to occur in higher abundance over deep slope areas and have been found to spawn over the continental slope in the North Atlantic [75]. In the eastern North Atlantic, Taonius pavo has been found from 28° to 47° N [78]. Collectively, these cephalopods show a latitudinal trend in diversity whereby the number of species approximately doubles from higher latitudes approximately 60°N to lower latitudes around 30°N [78, 79]. Cuvier's beaked whale movements may be influenced by this latitudinal increase in prey diversity.

The lack of a conclusive diel pattern in Cuvier's beaked whale clicks suggests that, in this continental slope region, they forage at similar rates throughout the day and night as the majority of Cuvier's beaked whale acoustic activity has been linked to foraging dives [54]. Previous work on diel acoustic behaviour of beaked whales has revealed a range of results. Unknown beaked whales off the Hawaiian islands of Kauai and Ni'ihau and beaked whales, including Cuvier's, recorded in the Cross Seamount of Hawaii clicked predominantly at night [15, 80, 81]. A more common finding is that beaked whales have different diel clicking behaviour depending on location and time of year [12, 14, 15]. For example, in the Ligurian Sea, Giorli et al. [14] described Cuvier's beaked whales foraging more at night through July, early August, and September, but in late August, October, and November there was no diel pattern. Furthermore, Giorli et al. [12] monitored three sites around the island of Hawaii and found that beaked whales clicked more at night at one site, more during the day at another, and had no diel pattern at the third site. While beyond the scope of our current work, further investigation into the present data at a station-specific and time-specific level could be revealing.

Cuvier's beaked whale clicks were particularly common off the northwestern slope of Porcupine Bank, a finding counter to a potential southern bias in distribution. Previous work in this Atlantic Margin region highlighted the potential importance for cetacean diversity of the northern and western margins of the Porcupine Bank [33]. The oceanography of this continental slope area leading into the eastern Rockall Trough may be uniquely productive and habitat modelling in the future could be revealing.

Strandings of Cuvier's beaked whales in Ireland are highest in spring and early summer and lowest in winter [82]. This led to an earlier hypothesis that Cuvier's beaked whales move northward into Irish waters between January and March to the northern limits of their range



in spring and summer [82]. Our data do not support such a migration as Cuvier's beaked whale occurrence was constant regardless of time of year except for October to December in 2015 when the species' occurrence increased as winter approached, particularly off the northwest slope of the Porcupine Bank. The results suggest that through late autumn 2015, individuals from outside of our monitoring areas moved into the northwest Porcupine Bank slope region, possibly driven by increased prey, or less likely, that the animals already in the area began producing more clicks. PAM data through the entire winter is required to further explore Cuvier's beaked whale temporal occurrence in the Atlantic Margin.

Prior to this study, Sowerby's beaked whale occurrence in Irish waters was largely unknown and had been limited to a small number of visual sightings [33, 47, 83, 84]. We confirm Sowerby's beaked whale presence and provide the first description of their occurrence across the slopes of the Atlantic Margin throughout the monitored periods. The preference of Sowerby's beaked whales for northern stations observed here is in agreeance with findings from an extensive North-East Atlantic visual survey which suggested that the species is more prominent north of 57°N [4]. Indeed, it seems that Sowerby's beaked whale densities are higher north of 50°N in the eastern North Atlantic, although sporadic sightings in the Bay of Biscay [4] and in the Canary Islands [85] indicate that the species' overall range extends further south. Sowerby's beaked whale spatial occurrence deviated from the generalised northern distribution at the northwest margin of the Porcupine Bank where, like Cuvier's beaked whales, occurrence was notably high.

The distribution of Sowerby's beaked whales is likely linked to prey that are typically smaller than those of Cuvier's beaked and Northern bottlenose whales [86]. In European waters, fish are their major prey item with Gadidae and Merlucciidae being the most important [73, 87, 88], though *Micromesistius poutassou*, *Trisopterus luscus/minutus* and *Merluccius merluccius* have also been identified as significant prey in the Bay of Biscay [87]. The increased Sowerby's beaked whale clicks during hours of darkness is likely driven by prey availability since daily variations in the vertical distribution of offshore pelagic fish species is well documented [89]. For example, *Merluccius merluccius*, *Micromesistius poutassou and Trisopterus* species undergo diel vertical migration and travel from the seabed to the surface at night [89–91]. As mentioned, beaked whale nighttime foraging has been reported previously [15, 80, 81].

Sowerby's beaked whale occurrence was constant through much of the 2015 and 2016 monitoring periods, apart from a large peak in May 2015 at the northernmost stations and a subtler peak in Nov 2015 along the northern Porcupine Bank slope. These findings support previous suggestions that at least some Sowerby's beaked whales move northwards in late winter and spring and southwards in the autumn [82], though our lack of data over the entire study area during the same time-frame limits our ability to make conclusive migratory conclusions.

The infrequent occurrence of northern bottlenose whales in the present study reflects previous findings as fewer than ten sightings of this species have been recorded along Ireland's Atlantic Margin [3, 4, 47, 92]. Northern bottlenose whale occurrence in Ireland is mostly known from occasional stranding events, the majority of which have occurred between the months of July and October, a similar time-frame as the clicks detected in our data [82]. In the North-East Atlantic, Northern bottlenose whales are thought to undertake annual migrations. They move to Arctic waters in spring to forage on newly hatched cephalopods (*Gonatus fabricii*) that do not occur south of 55 °N [72, 75] and, in early autumn, they return to temperate waters to forage on Cranchiidae such as *T. pavo* and *Teuthowenia megalops* [86, 93, 94]. The continental slope habitats monitored in this study do not appear to be part of the core habitat of the species in this part of the North-East Atlantic. One plausible scenario is that the Atlantic Margin lies at the boundary of the species' current distributional range and is therefore only occasionally frequented by migrating or foraging individuals. The majority of Northern bottlenose whales may occur further offshore in the deeper waters of the Rockall Trough where the



species has been more regularly sighted [4] and detected acoustically [95]. The steep eastern slope of the Rockall Bank may also offer a suitable habitat for this species [96, 97].

The absence of Gervais' and True's beaked whale clicks in our data indicates that these species were either truly absent from the region or that they occur in the region but were not identified in the acoustic analyses. Both species are known in Irish waters from very rare instances [33, 40]; thus, the former may be the case, but we cannot rule out the latter. Indeed, the acoustic signals of Gervais' beaked whales are poorly understood and True's beaked whale clicks have yet to be described. Our automated detector was not trained to detect these species and given that manual analysis was driven by automated detections, acoustic signals of these species may well have occurred in files that went unanalyzed. As new research on the repertoire of beaked whales continues to emerge, this dataset can be revisited in the future to more confidently determine the presence or absence of Gervais' and True's beaked whales in the Atlantic Margin.

Though not the aim of the present study, it is nevertheless pertinent to describe the anthropogenic sounds we encountered during analysis given the risks that some human activities can introduce to beaked whales [17–26]. The seismic impulses recorded in 2015 were produced by an unknown seismic exploration program, likely distant and offshore. In 2016, seismic impulses were produced by a licensed seismic exploration program for hydrocarbons in the Porcupine Seabight that occurred 165 to 230 km from stations 3 and 5 to 8. Seismic occurrence was most frequent at stations 7 and 8, at the mouth of the Porcupine Seabight, (Fig 11) because the other stations were shadowed by the shelf. The absence of a discernable Cuvier's and Sowerby's beaked whale acoustic behavioural reaction in terms of click presence/absence and the low level of received seismic energy suggests little impact from seismic activity at these received levels [98]. The detection of naval sonar pulses was of concern, due to its association with previous stranding events by deepdiving species. The use of naval sonar was opportunistically observed during three periods in the autumn of 2015: 17–18 Sept at Stations 1–4, 7–10 Oct at Stations 1–4, and 19–20 Oct at Stations 1 and 2 (Fig 11). Detailed acoustic behavioural response analysis for seismic airguns and the sonar pulses was beyond the scope of our work, but should be explored in the future.

While PAM on the Atlantic Margin has allowed us to document the occurrence of elusive beaked whales at relatively low effort and cost in a remote offshore region, PAM has limitations. The bottom-mounted acoustic recorders are likely only detecting clicks during deep foraging dives. Thus, missing animals in the area, but at the surface, those who dive but do not actively echolocate, or those who click at an angle or distance from the recorder such that the received clicks cannot be identified by either the automated detector or analysts. Therefore, the results presented here represent a minimum occurrence of these species in offshore Irish waters. Given the broad spatio-temporal scale of our data, the potential influence of fluctuations in dive rate, click rate, and animal movements in or out of the detection area should be negligible, as the resulting upward or downward biases on detection rates should even out over time. This assumes a similar use of the habitat surrounding the recording locations, since differences in dive and click rate as well as residency patterns may be associated with differences in habitat use [12]. Therefore, despite the accepted limitations of PAM for odontocete clicks, we believe that these results depict an accurate picture of the relative occurrence of beaked whales across the monitored stations and can be used as a baseline for future assessments of occurrence and habitat use.

Conclusions

The findings presented here highlight the hitherto unknown importance of the Atlantic Margin for Cuvier's and Sowerby's beaked whales and provide the first insights into potential range differences, with each species respectively favouring slope areas in the southern and



northern parts of the study area, a pattern likely driven by preferred prey distributions. In contrast, northern bottlenose whales only occurred sporadically in the late summer and early autumn. All observed species showed preference for the northwest margin of Porcupine Bank, highlighting a potentially important biological region in need of further research. Our acoustically-derived results are in stark contrast to the scarcity of sightings of beaked whales off Ireland from traditional ship- or boat-based survey methods, which strongly supports the use of static acoustic monitoring as a reliable method for detecting these elusive species. Given the known sensitivity of these animals to some anthropogenic sounds, our findings should be given appropriate consideration when assessing the environmental risks and management actions required for any expansion of human activities in Ireland's Atlantic Margin.

Supporting information

S1 Dataset. Period1, station1 automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S2 Dataset. Period 1, station1 automated detections for Sowerby's beaked whales. (CSV)

S3 Dataset. Period 2, station2 automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S4 Dataset. Period 2, station3 automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S5 Dataset. Period 2, station4 automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S6 Dataset. Period 1, station2 automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S7 Dataset. Period 1, station2 automated detections for Sowerby's beaked whales. (CSV)

S8 Dataset. Period 1, station4 automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S9 Dataset. Period 1, station4 automated detections for Sowerby's beaked whales. (CSV)

S10 Dataset. Period 2, station1 automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S11 Dataset. Period 2, station1 automated detections for Sowerby's beaked whales.

S12 Dataset. Period 2, station2 automated detections for Sowerby's beaked whales. (CSV)



S13 Dataset. Period 2, station3 automated detections for Sowerby's beaked whales. (CSV)

S14 Dataset. Period 2, station4 automated detections for Sowerby's beaked whales. (CSV)

S15 Dataset. Period 3, station3 automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S16 Dataset. Period 3, station5 automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S17 Dataset. Period 3, station6 automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S18 Dataset. Period 3, station7 automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S19 Dataset. Period 3, station8 automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S20 Dataset. Period 3, station3 automated detections for Sowerby's beaked whales. (CSV)

S21 Dataset. Period 3, station5 automated detections for Sowerby's beaked whales. (CSV)

S22 Dataset. Period 4, station7 automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S23 Dataset. Period 4, station8 automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S24 Dataset. Period 4, station5 automated detections for Sowerby's beaked whales. (CSV)

S25 Dataset. Period 4, station6 automated detections for Sowerby's beaked whales. (CSV)

S26 Dataset. Period 4, station 7 automated detections for Sowerby's beaked whales. (\mbox{CSV})

S27 Dataset. Period 4, station 8 automated detections for Sowerby's beaked whales. (\mbox{CSV})

S28 Dataset. Period 3, station6 automated detections for Sowerby's beaked whales. (CSV)

S29 Dataset. Period 3, station7 automated detections for Sowerby's beaked whales. (CSV)



S30 Dataset. Period 3, station 8 automated detections for Sowerby's beaked whales. (\mbox{CSV})

S31 Dataset. Period 4, station5 automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S32 Dataset. Period 4, station6 automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S33 Dataset. Manual verification of automated detections for Cuvier's beaked and northern bottlenose whales.

(CSV)

S34 Dataset. Manual verification of automated detections for Sowerby's beaked whales. (CSV)

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