



Seasonal and diel patterns in cetacean use and foraging at a potential marine renewable energy site

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ABSTRACT

Marine renewable energy (MRE) developments often coincide with sites frequented by small cetaceans. To understand habitat use and assess potential impact from development, echolocation clicks were recorded with acoustic click loggers (C-PODs) in Swansea Bay, Wales (UK). General Additive Models (GAMs) were applied to assess the effects of covariates including month, hour, tidal range and temperature. Analysis of inter-click intervals allowed the identification of potential foraging events as well as patterns of presence and absence. Data revealed year-round presence of porpoise, with distinct seasonal and diel patterns. Occasional acoustic encounters of dolphins were also recorded. This study provides further evidence of the need for assessing temporal trends in cetacean presence and habitat use in areas considered for development. These findings could assist MRE companies to monitor and mitigate against disturbance from construction, operation and decommissioning activities by avoiding times when porpoise presence and foraging activity is highest in the area.

1. Introduction

Marine renewable energy (MRE) has the potential to reduce fossil fuel dependency in coastal nations with appropriate tidal and wave energy resources (Manasseh et al., 2017). To utilise these resources in South West Wales (UK), a tidal lagoon development has been proposed for the inner Swansea Bay that encompasses an area of 11.5 km² with a 9.5 km² breakwater designed to harness electricity from the natural ebb and flow of the ocean tide, using submerged hydro turbines. Swansea Bay has a large natural tidal range, the second highest in the world, with a difference of up to 10.5 m making it an ideal site for MRE development. The Swansea Bay Tidal Lagoon will be a unique construction and the world's first tidal lagoon power plant with an estimated > 530 GWh net power output capacity capable of powering 155,000 homes annually. Recent increases in MRE construction and operation, particularly of windfarms but also of wave and tidal devices, pose a potential threat to many cetacean populations (Brandt et al., 2011; Carstensen et al., 2006; Dähne et al., 2013). These include disturbance from construction and operation noise and increased boat traffic in the area; risks of collision and entanglement; potential loss of habitat and adverse effect on prey species (Dolman and Simmonds, 2010; Simmonds and Brown, 2010; Wilson et al., 2007).

The most common cetacean species in European waters, and thus the most likely species to be affected by MRE development is the harbour porpoise (*Phocoena phocoena*) (Baines and Evans, 2012; Reid et al.,

2003). Although protected by the EU Habitats and Species Directive, which requires the monitoring of its conservation status, little is known about the habitat use or residency patterns of this evasive cetacean species (Embling et al., 2010). Without distinct markings, it is difficult to identify individuals and ascertain home ranges for such a mobile species (Embling et al., 2010). Satellite tagging studies from Denmark show remarkably long distance travel paths for the Baltic harbour porpoise (Sveegaard et al., 2012) and there is no evidence to suggest that the same would not be true for porpoise in UK waters. Previous studies have found evidence of seasonal and diurnal patterns in the occurrence of harbour porpoise with greater detections at night albeit with distinct spatial variations often attributed to prey availability (Carlstrom, 2005; Schaffeld et al., 2016; Todd et al., 2009). Harbour porpoise are known to be opportunistic feeders and foragers and many studies have highlighted the importance of sediment substrate and water depths on their distribution and behaviour and feeding patterns (Brandt et al., 2014; Brookes et al., 2013; Mikkelsen et al., 2013; Todd et al., 2009; Williamson et al., 2016). For example, Williamson et al. (2017) studied diurnal variation in harbour porpoise detection based on sediment type and water depth in Moray Firth, Scotland, and found increased foraging behaviour in muddier, deeper habitats at night but increased diurnal patterns in shallower sandy habitats overall. In addition, the tidal flow is also an important determinant of porpoise distribution in high energy environments, where acoustic encounters of porpoises have been shown to vary significantly at very small

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spatiotemporal scales (Benjamins et al., 2017). A better understanding of the fine scale seasonal and diurnal patterns in distribution will provide more insight into habitat use by these small cetaceans, and provide the evidence needed to protect them against potential anthropogenic impacts.

Previous visual and acoustic studies have shown year-round presence of porpoises in Swansea Bay with possible summer peak in frequency of observations (Baines and Evans, 2012; Watkins and Colley, 2004), although typically the area is thought to be less frequented by the species in comparison to ‘hotspots’ in Welsh waters, such as West Pembrokeshire and Cardigan Bay (Baines and Evans, 2012). The harbour porpoise population in Swansea Bay is generally considered to be part of the Celtic Sea management unit which spans across the Irish Sea, Celtic Sea, Western English Channel and Southwest Ireland (Evans, 2012). Recently a candidate Special Area of Conservation (SAC) was proposed for the Bristol Channel Approaches for harbour porpoise during winter season but this did not include Swansea Bay within its boundaries (JNCC, 2016).

1.1. Rationale for acoustic monitoring

Visual surveys, whether land, aerial or boat-based are particularly limited by daylight, weather conditions and visibility (Evans and Hammond, 2004). Static acoustic monitoring (SAM) is a widely used to complement visual methods and are typically used to describe fine-scale temporal patterns in habitat use for vocalising cetaceans (Brookes et al., 2013; Thompson et al., 2015; Williamson et al., 2017). Data recorders, such as C-PODs, enable continuous monitoring throughout the diel cycle, in all seasons and in adverse weather conditions (Simon et al., 2010), although high levels of noise in the recording frequency band (such as heavy rain, or dolphin echolocation right next to a data logger) may cause the recorder's memory to fill up (Tregenza, 2014). Static devices can be used to understand fine scale temporal patterns otherwise missed by visual surveys, although they can have limited spatial coverage (Brookes et al., 2013), unless resources allow for the deployment of numerous devices.

Echolocation click signals can be recorded using bottom moored, automated underwater click loggers called C-PODs (Chelonia Ltd., Cornwall, UK, www.chelonia.co.uk), which autonomously log times and characteristics of echolocation clicks. The loggers detect echolocation clicks between 20 and 160 kHz, and can be used to study presence, relative abundance, foraging behaviour, habitat use and distribution of cetacean species (Benke et al., 2014; Berrow et al., 2009; Carlstrom, 2005; Nuuttila et al., 2013a, 2013b; Pirodda et al., 2014; Rayment and Dawson, 2009; Schaffeld et al., 2016; Simon et al., 2010; Verfuß et al., 2007) and have been widely used to assess anthropogenic disturbance from wind farms, shipping, fisheries and coastal development (Carlstrom, 2005; Carstensen et al., 2006; Cox et al., 2001; Todd et al., 2009).

Clicks are logged if they show a sufficiently high peak sound pressure level and a distinct spectral peak in the frequency range covered. Specific software classifies detected sounds into sequences called click trains. These are further categorised based on their likely origin (boat sonar, dolphin, or porpoise click trains) according to known characteristics. Harbour porpoises and most delphinids produce high frequency clicks for navigation as well as prey detection and discrimination and prey capture. Echoes provide information on the range of their prey targets and allow the animals to detect objects outside their visual range (Au and Fay, 2000). Porpoises echolocation signal is highly stereotypical, containing very short clicks (50–150 µs) and very little energy below 100 kHz (Au et al., 1999; Teilmann et al., 2002; Villadsgaard et al., 2007). The main part of the energy is within a narrow band of 120–150 kHz, making them ideal for automatic acoustic detection, since most other noise in the sea usually contains energy over a wider frequency range, is of much longer duration, and has peak energy at much lower frequencies. Furthermore, porpoise echolocation

clicks have decreasing or increasing temporal pattern whereas most other noise in this frequency band (i.e. boat echo sounders) produce very regular clicks (Teilmann and Carstensen, 2012). Delphinid clicks can also be detected by C-PODs, and they can be distinguished from porpoise clicks as they are shorter, more varied, with much higher source levels and have energy across a wider frequency band (Au et al., 1974; Au and Hastings, 2008; Wahlberg et al., 2011). Dolphins, do not, however, always echolocate and therefore have a lower probability of being detected as compared to porpoises (Nuuttila et al., 2013a; Philpott et al., 2017), who echolocate almost continuously (Akamatsu et al., 2007; Linnenschmidt et al., 2013). Presence of dolphins can affect porpoise acoustic behaviour and interfere with performance of the acoustic dataloggers. It was therefore necessary to ascertain dolphin presence in the study area. From opportunistic land based observations and from local boat trip operators we also know that occasional sightings of common dolphins (*Delphinus delphis*) and bottlenose dolphins (*Tursiops truncatus*) have been made in the area (Robinson, Sea Watch Foundation, pers. comm.). Recent photographic evidence confirms a group of Risso's dolphins (*Grampus griseus*) spotted off Mumbles headland, west side of Swansea Bay (Hunt, pers. comm.).

The aim of this study was to use static acoustic dataloggers to explore temporal patterns in cetacean habitat use and foraging in and around the proposed Swansea Bay Tidal Lagoon development site. This information is crucial for assessing potential risks to cetaceans from the tidal lagoon as well as mitigating against them to ensure successful development of MRE infrastructure in Wales. Perceived threats to cetaceans from most MRE devices and structures are linked to collision risk, entanglement and displacement due to habitat loss and/or prey depletion (Dolman and Simmonds, 2010; Simmonds and Brown, 2010). Here we show the importance of understanding localised patterns in habitat use to assess potential impacts of MRE developments on cetaceans in coastal waters.

2. Materials and methods

2.1. Study area

Swansea Bay (Wales, UK) is a large sweeping sandy bay located on the northern coastline of the Bristol Channel with a depth of < 20 m OD (Fig. 1) (Pye and Blott, 2014). The bay is a shallow embayment with an anticyclonic gyre and a rectilinear current offshore dominated by refracted waves from the southwest (Davies, 1974). The geology of the bay is largely characterised by relict Pleistocene bed sediments overlain by unconsolidated and poorly sorted glacial till, pebbles, sand and silt and a large area of the outer Swansea Bay is a historic dredge spoil ground from the local docks. At Mean Low Water (MLW) approximately 618 ha of intertidal mudflats and sand bars are exposed. Water quality is largely influenced by the hydrology of the three river catchments (Tawe, Neath and Afan) serving Swansea Bay in addition to historical and current diffuse pollution.

The Swansea Bay Tidal Lagoon site location (Fig. 1) is situated between the River Tawe and Neath connecting the Swansea Docks in the west to the Swansea University Bay Campus in the east. The development encompasses the main sewage outfall, southwards of Swansea Docks, of the Swansea catchment, an area which is known to be frequented by harbour porpoise.

2.2. Deployment sites

Acoustic data loggers were deployed in four locations in the Swansea Bay area (Fig. 1); inside the proposed lagoon site, by a sewage outfall pipe (‘Outfall’), east of Mumbles, (‘Mumbles’), outside the Swansea Bay, in Oxwich Bay (‘Oxwich’) and offshore, in Scarweather sandbank (‘Scarweather’). The sites were selected away from main shipping lanes and dredging and fishing areas and to maximise likelihood of porpoise detections. The deployment site coordinates, average

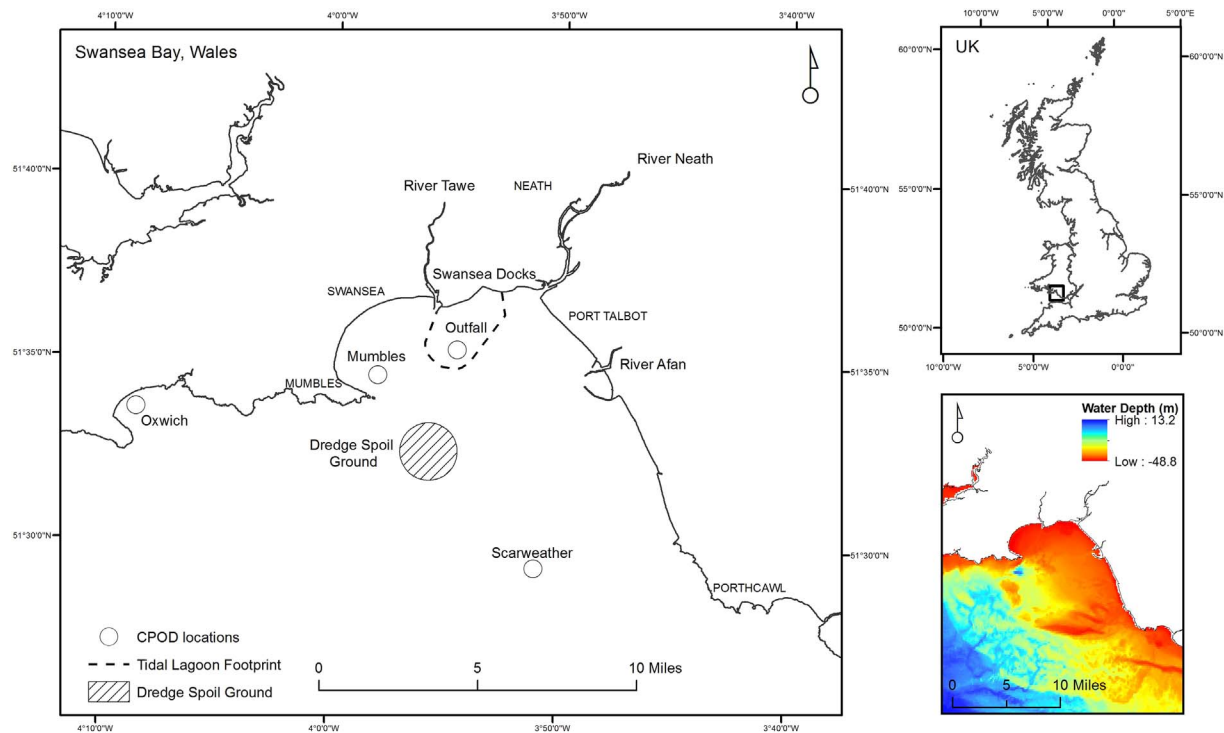


Fig. 1. Location of the four C-POD deployment sites in Swansea Bay showing the proposed MRE tidal lagoon footprint. The inset maps display water depth (m) in Swansea Bay and the study area in the context of the UK.

Table 1
C-POD deployment details.

Location	Longitude (decimal degrees)	Latitude (decimal degrees)	Max water depth (m) ^a	Sediment type (Wentworth-Udden scale, Callaway, 2016)	Deployment period	No. of days deployed
Outfall	3.901084	51.597663	15.7	Granule + very coarse sand	Feb-14 to Jul-15	502
Mumbles	3.951098	51.580994	14.6	Fine + medium sand	Feb-14 to Jul-15	433
Oxwich	4.134485	51.547653	14.7	Fine sand	Feb-14 to Feb-15	267
Scarweather	3.834403	51.480966	19	Fine sand	Dec-14 to Jan-15	38

^a Chart datum + maximum spring high tide range, 10.4 m (average tidal range at spring tides is 8.5 m).

water depths and deployment durations are listed in Table 1.

2.3. Data loggers

Eight C-PODs were used in this study. The manufacturer adjusted the click loggers to a standard sensitivity threshold at a tank facility, and a further field calibration was conducted *in-situ* at one of the recording locations for a period of 8 days. One of the dataloggers recorded significantly more clicks than the others during the field calibration period and was sent back to the manufacturer for re-adjustment. Initially the dataloggers were moored using acoustic releases (Sonardyne Lightweight Acoustic Release Transponders or LRTs) but these did not perform as well as expected. There were several occasions when the acoustic releases used for deployment were accidentally and the C-PODs floated to the surface and eventually to the shore. All the loggers that were released prematurely were successfully recovered and subsequently sent back to the manufacturer for recalibration before being redeployed. Despite assistance from the manufacturer, it was not possible to avoid this. The C-PODs were attached to a weighted ground line, in a position approximately 1.5 m above triggered seabed. This line was connected surface markers away from the C-POD to avoid movement and excessive noise.

2.4. Data analysis

Acoustic data were downloaded with C-POD.exe software (v.2.044; Chelonia Ltd., Cornwall, UK, www.chelonia.co.uk). The in-built click train detection algorithm filters through the raw click data, identifies cetacean click trains and assigns them into quality categories, depending on their probability of arising by chance from a non-train producing source (such as rain or a boat propeller). It then classifies them by categories depending on click and click train characteristics. These include narrow-band high frequency (‘NBHF’) click trains, such as harbour porpoise click trains and generic dolphin type click trains (‘Other cet’). To minimise false positive detections only data classified as having a high likelihood of being of porpoise or dolphin origin (‘High’ and ‘Mod’ quality classes) was used for the analysis. Although this meant that some real detections were missed, this was considered more desirable than to include potential false positive detections in the analysis.

Sunrise and sunset times (from civil twilight) as well as highwater times and tidal ranges were obtained from the POLTIPS tidal prediction program (version 3.6.0.0/13, Bell, 2016). The co-variables used for the initial analysis were selected to allow assessment of diel, seasonal and tidal variation in habitat use. These were month, time from nearest high water (HW_Diff), tidal range for the day (HW_Range), sea water temperature recorded by the C-POD, time from sunrise (Sunrise_Diff) and time from sunset (Sunset_Diff). C-POD location was included to

evaluate difference between different sites. The total number of clicks recorded (NAllClicks) was included to assess the effect of noisy conditions on animal detections due to logger performance. The angle of the C-POD from vertical was included to allow assessment of the effect of logger position in the water column on detections. All covariates were analysed as smooth variables (f) apart from location which was treated as a factor variable (F).

$$E[\text{DPM}/h_i] = f(\text{Month}) + f(\text{HWDiff}) + f(\text{HWRRange}) + f(\text{Temp}) \\ + f(\text{SunriseDiff}) + f(\text{SunsetDiff}) + f(\text{NAllClicks}) \\ + F(\text{Location}) \quad (1)$$

The data were analysed for every hour and the response variables used were the number of minutes with porpoise and dolphin detections for each hour (0–60 Detection Positive Minutes or DPM) and the number of foraging buzzes ($\text{ICI} < 10 \mu\text{s}$) recorded per hour. All statistical analyses were conducted with R version 3.3 (R Development Core Team 2013) and R Studio version 1.0.136 (RStudio Team 2015). The covariates were tested for collinearity using the *vif* function in package *car*, with 2 as the cut-off value. Autocorrelation of the response variables were assessed using Durban Watson test and ACF plots with package *itsadug* (van Rij et al., 2016). The data were found autocorrelated. Due to the time it took to run the analyses for the large dataset we used the function *bam* in the *mgcv* package to conduct Generalised Additive Models (GAMs) with negative binomial error distribution (*negbin*) to mitigate against the effect of overdispersion in the data and an autoregressive (AR) correlation structure to account for the autocorrelation (Wood, 2011; Wood et al., 2015). The *bam* function allows sub-blocks of model matrix to be computed at a time, simplifying the complex modelling problems associated with working with datasets with tens of thousands of data points (Wood et al., 2015). Both Generalized Cross-validation (GCV) and manual knot selection was used, with final values selected visually based on the trade-off between simplicity of the model and explanatory power of the smooth graphs (see all model summaries in the Online Supplement 1). The ρ values for the AR structure were calculated with the *itsadug* package and the function *gam* was used to acquire the θ values required for the *negbin* distribution. The R script for the autocorrelation with corrected ACF plots together with the modelling results, are available in the Online Supplement 2. The variable hour was found to be collinear with time from sunrise and sunset, and was removed from the base models. No interaction terms were included in the models as these had only negligible effect on the model results. Only those hours where full recordings were made were selected for analysis. Excessively noisy data was excluded by removing all data with $> 5\%$ time lost due to noise as assessed by C-POD exe (% Time Lost). The diagnostic plots to assess model fit are not particularly useful for negative binomial models and the adjusted R^2 values can be difficult to interpret. p -Values for each covariate from the *bam* summaries were used to assess whether variables should be retained in the final model (Murtaugh, 2014) (Table 2 and the Online Supplement 1). In addition, to assess the effect of each covariate in the final model, each variable was removed one at a time from the full model and the Akaike's Information Criterion (AIC) values, the deviance explained and the adjusted R^2 values were inspected to assess the effect of each covariate and the overall model fit (Table 3).

2.5. Foraging click trains

Only harbour porpoise data was used for the foraging analyses. In keeping with earlier studies click trains were classified as foraging buzzes if they had at least one inter-click interval (ICI) of $< 10 \mu\text{s}$ (Carlstrom, 2005; Linnenschmidt et al., 2013; Nuuttila et al., 2013a; Todd et al., 2009; Verfuß et al., 2009). These were further inspected for presence of a sudden decrease in ICI, defined as 2/3 decrease in the ICI values within a train (Schaffeld et al., 2016). To assess the effect of the additional criterion, GAM analyses were run on click trains that fit the

traditional condition of $10 \mu\text{s}$ ICI cut off as well as those click trains that fit both criteria, with all the same co-variables as with the DPM analyses.

$$E[\text{HP Foraging}/h_i] = f(\text{Month}) + f(\text{HWDiff}) + f(\text{HWRRange}) + f(\text{Temp}) \\ + f(\text{SunriseDiff}) + f(\text{SunsetDiff}) + f(\text{NAllClicks}) \\ + F(\text{Location}) \quad (2)$$

The additional criterion of a sudden decrease in the ICI reduced the dataset drastically but did not have a noticeable effect on the significance of the smooth terms or the curves of the smooth plots. Therefore, the single criterion of $\text{ICI} < 10 \mu\text{s}$ was used as to define foraging in this dataset. The results for both approaches are listed in the GAM/BAM summaries listed in the Online Supplement 1.

3. Results

The study yielded recordings from 614 days comprising a total of 1225C-POD days of recordings from the four sites between February 2014 and December 2015. The Mumbles and Outfall sites had data loggers deployed over twelve months, whereas the Oxwich site had a logger deployed for only nine months. The Scarweather loggers only recorded for less than a month and were removed from the analysis. In total, there were 550 days with porpoise detections and 465 days logged with foraging clicks. Loggers at Outfall detected porpoises 430 out of 503 days (85%), at Mumbles 324 out of 433 (75%) and Oxwich 213 out of 267 (78%) (Fig. 2). In contrast, there were only 28 days with dolphin detections at Outfall, 46 at Oxwich and 19 days at Mumbles (see also Online Supplement 2).

3.1. Harbour porpoise detections

Detection rates of harbour porpoises were consistently higher than those of dolphins throughout the sampling period, although both depicted clear seasonal variation. The final and best model included all co-variables apart from tidal range (Table 2).

$$E[\text{DPM}/h_i] = f(\text{Month}) + f(\text{HWDiff}) + f(\text{Temp}) + f(\text{SunriseDiff}) \\ + f(\text{SunsetDiff}) + f(\text{NAllClicks}) + F(\text{Location}) \quad (3)$$

Table 3 lists the results of removing each covariate from the full model to assess the effect of each variable. The AIC values and the deviance explained depicted all clicks, temperature, location and month as the most influential co-variables for porpoise presence, followed by time from sunrise, time from sunset and angle of the C-POD, whilst time from high water had only a negligible effect predicting porpoise detection. Deployment location had a clear effect of location on porpoise detections, with the dataloggers at Outfall and Oxwich recording much higher number of clicks on average than loggers at Mumbles (Fig. 3).

Porpoise foraging clicks were positively correlated with detection positive minutes (Pearson Product Moment coefficient $r = 0.77$). The final and best model included month, time from sunrise, time from sunset, temperature and all clicks as smooth variables and location as a factor variable (Table 2). For this model, all clicks and month were the most influential covariates (Table 3). GAM/BAM summaries and the associated R code are detailed in the Online Supplement 1.

$$E[\text{HP Foraging}/h_i] = f(\text{Month}) + f(\text{SunriseDiff}) + f(\text{SunsetDiff}) \\ + f(\text{Temp}) + f(\text{NAllClicks}) + F(\text{Location}) \quad (4)$$

3.2. Seasonal variation

In general, both porpoise detections as well as foraging buzzes reached a peak in late summer, between August and October (Figs. 3 & 4) although variation in the seasonal pattern of detections between the sites was evident (Fig. 5). The site at Oxwich exhibited the highest average number of minutes with detections per hour (DPM/h)

Table 2

A. Final model summary for harbour porpoise detections. B. Final model summary for harbour porpoise foraging clicks.

Smooth terms	edf	df	F-value	p-Value	Parametric coefficients	Estimate	Std error	T-value	p-Value
A									
Month	3.902	4.00	40.246	< 0.001	Intercept	− 0.17663	0.12252	− 1.442	0.149
Sunrise	3.239	4.00	8.733	< 0.001	Location (Outfall)	1.04261	0.07871	13.246	< 0.001
Sunset	3.598	4.00	29.786	< 0.001	Location (Oxwich)	0.82296	0.09477	8.684	< 0.001
Highwater	2.292	2.684	3.336	0.0167					
Temperature	4.871	4.992	38.625	< 0.001					
NAllClicks	4.901	4.994	166.927	< 0.001					
Angle	4.170	5.138	6.162	< 0.001					
B									
Month	3.727	4.00	31.699	< 0.001	Intercept	1.8998	0.1890	10.050	< 0.001
Sunrise	2.988	4.00	4.798	< 0.001	Location (Outfall)	1.3433	0.1353	9.930	< 0.001
Sunset	3.307	4.00	17.653	< 0.001	Location (Oxwich)	0.2854	0.1652	1.728	0.0841
Temperature	4.644	4.943	15.549	< 0.001					
NAllClicks	4.935	4.997	203.168	< 0.001					

A) R-sq. (adj) = 0.0651, deviance explained = 15.3%, fREML = 27,947, Scale est. 0.99076, n = 26,162. B) R-sq. (adj) = − 1.19e + 10, deviance explained = 22.2%, fREML = 32,672, Scale est. = 1.8348, n = 26,020.

with peaks of detections recorded in spring (March 5.60 DPM/h, April 6.54) DPM/h and a dip in detections between June and August. The Outfall site received second highest detections in late summer and early winter (August 3.58 DPM/h, November 4.07 DPM/h) in comparison to average monthly detection (1.63 DPM/h). Detections in Mumbles depicted a different pattern to the two, with much lower detections in general with little pattern, apart from a higher DPM in the month of November (1.23 DPM/h) in comparison to the site average (0.45 DPM/h) (Fig. 5).

3.3. Diel and tidal variation

There was an increase in porpoise detections during and after sunset which varies approximately between 16:00 and 21:30 during the sampling period (Fig. 6). This applied to both general detections as well as foraging buzzes. Loggers at Oxwich and Outfall recorded higher hourly detection rates than Mumbles. Tidal range was not a significant covariate. Time from high water was found significant predictor for porpoise detections but for foraging buzzes no significant effect of tidal

Table 3

The effect of each co-variate for all three datasets, using p-values from the full model and adjusted R² values, deviance explained and AIC values from the full model run without each covariate. Rank 1 denotes the most influential co-variate, rank 9 the least influential.

Porpoise covariate	p-Value*	Adj. R ² rank	Change in dev. expl	Change in AIC	AIC rank
All clicks	***	4	− 4	525.68	1
Temperature	***	1	− 3	394.81	2
Location	***	2	− 2.6	342.39	3
Month	***	3	− 3.7	420.88	4
Sunset	***	5	− 1.7	212.13	5
Sunrise	***	9	− 0.6	60.38	6
Angle	***	7	− 0.5	45.1	7
High water	*	6	− 0.2	8.46	8
Tidal range		8	− 0.1	3.51	9
Porpoise foraging covariate	p-Value*	Adj. R ² rank	Change in dev. expl	Change in AIC	AIC rank
All clicks	***	1	− 10.7	1234.57	1
Month	***	7	− 3.7	420.88	2
Temperature	***	6	− 2.3	262.80	3
Location	***	9	− 1.9	229.04	4
Sunset	***	4	− 2	224.31	5
Sunrise	***	8	− 0.4	43.69	6
Tidal range		5	− 0.2	22.04	7
Angle		3	0	− 7.10	8
High water		2	0.1	− 10.50	9
Dolphin covariate	p-Value*	Adj. R ² rank	Change in dev. expl	Change in AIC	AIC rank
Angle	.	2	− 23.7	207.5337	1
Month	***	1	− 11.6	29.802	2
Tidal range	.	5	− 6.9	− 39.0641	3
Temperature	**	3	− 6.7	− 42.084	4
Sunset		4	− 6.5	− 42.6724	5
Location	***	6	− 6.5	− 46.7592	6
All clicks	***	7	− 4.1	− 73.3997	7
Sunrise		8	− 3.9	− 74.241	8
High water		9	− 3.9	− 75.9607	9

*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

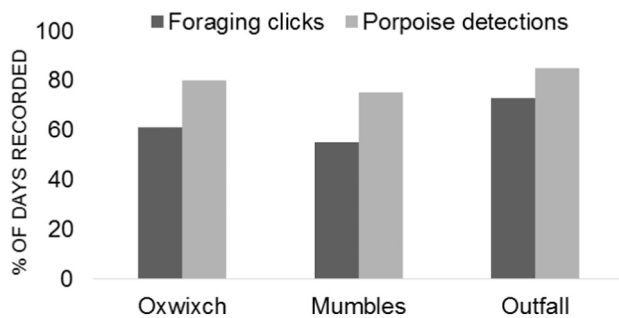


Fig. 2. Percentage of recording days with detections and foraging clicks at three sites in Swansea Bay across the sampling period.

cycle was found (Table 2).

3.4. Temperature and noise

The seawater temperature as recorded by the C-PODs had a significant effect on detections with water temperature around 10–11 °C predicting highest number of detections. Variable all clicks, used as a proxy for general noise conditions, was a significant covariate in all models. Typically an initial increase in clicks recorded would also indicate an increase in detections, but as the click levels kept cumulating, the detections would begin to fall.

3.4.1. Dolphin detections

Dolphin presence was relatively low compared to porpoise detections throughout the sampling period at all locations. The final model included all statistically significant variables: month, tidal range, temperature, all clicks and angle (Fig. 7.).

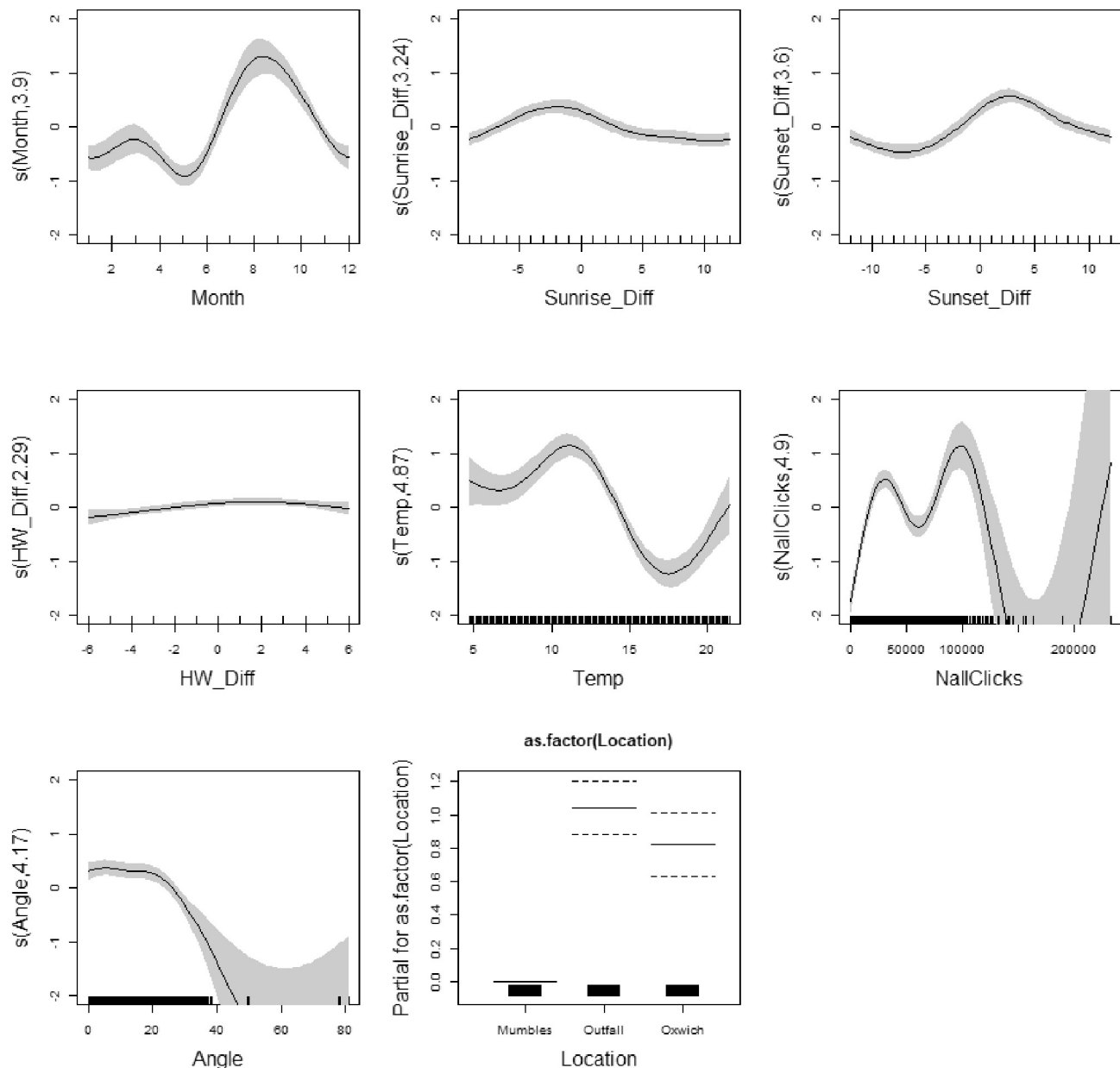


Fig. 3. Fitted relationships for the final harbour porpoise model based on GAM/BAM standard errors. The grey areas around the relationship are the 95% confidence intervals for each smooth covariate. For factor variables, this is represented by dotted lines. The y-axis shows the partial residuals for each model covariate generated by regressing the response on the other covariates.

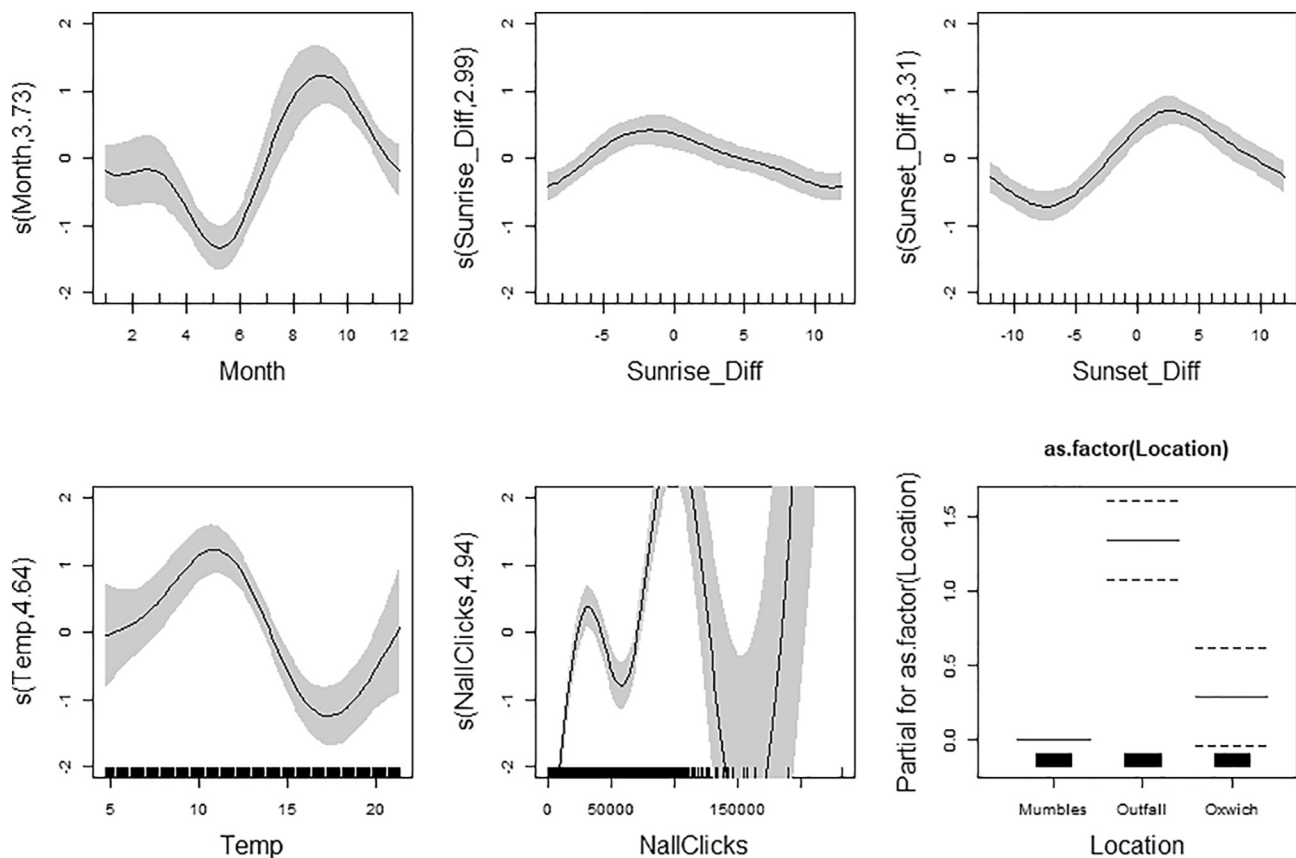


Fig. 4. Fitted relationships for the final harbour porpoise foraging click model based on GAM/BAM standard errors. The grey areas around the relationship are the 95% confidence intervals for each smooth covariate. For factor variables this is represented by dotted lines. The y-axis shows the partial residuals for each model covariate generated by regressing the response on the other covariates.

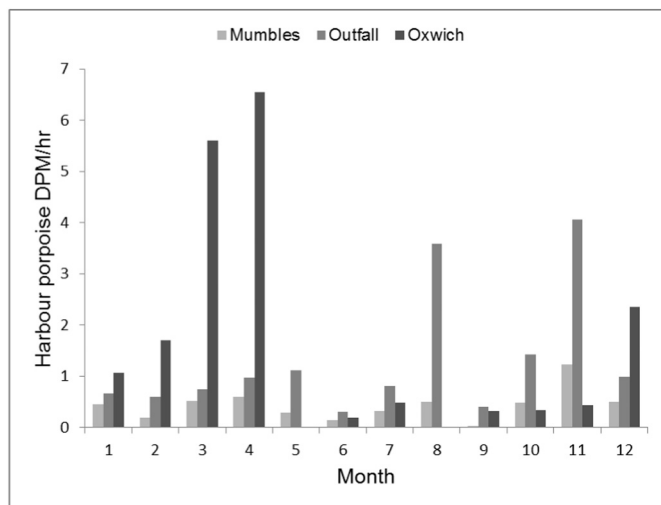


Fig. 5. Mean harbour porpoise detection positive minutes (DPM) per hour for each month and each CPOD monitoring location.

$$E[DPM/h_i] = f(\text{Month}) + f(\text{HWRRange}) + f(\text{Temp}) + f(\text{NallClicks}) + f(\text{Angle}) \quad (5)$$

To assess the effect of each covariate, these were removed one at a time from the full model. The resulting adjusted R_2 values and the change in AIC (ΔAIC) were compared with the p -values for individual variables in the full model (Table 3). Typically, the p -values and the AIC values of each model without a specific covariate would agree, but this was not the case here for most variables. Therefore, the evaluation of

the effect of covariates for the dolphin model was not conclusive, although the two methods agreed that month had a significant effect on dolphin detections and that time from highwater did not. Angle seemed to have the strongest effect on detections according to AIC rank, whereas according to p -values it is barely significant (Table 3).

3.5. Seasonal, diel and tidal variation

Dolphins showed highest detection rates in summer months (June to August) with some variation between sites, although location was not a significant variable. Dolphins depicted less of a diel pattern than harbour porpoise. No pattern was found with regards to the tidal cycle, although smooth plot showed some increase in detections with higher tidal ranges associated with spring tides (Fig. 7).

3.6. Temperature and noise

Just as with porpoise detection, seawater temperature and all clicks both had a significant effect on dolphin detections with similar patterns.

4. Discussion

4.1. Diel and seasonal patterns

In this study, acoustic monitoring was used to reveal a year-round presence of harbour porpoise in Swansea Bay as well as occasional visits from delphinids, which confirms the findings of previous acoustic and visual studies (Baines and Evans, 2012; Watkins and Colley, 2004). Harbour porpoise were recorded in the bay all year round with highest detections in summer and early autumn and during evening and night time coinciding with sunset. These patterns were evident in all

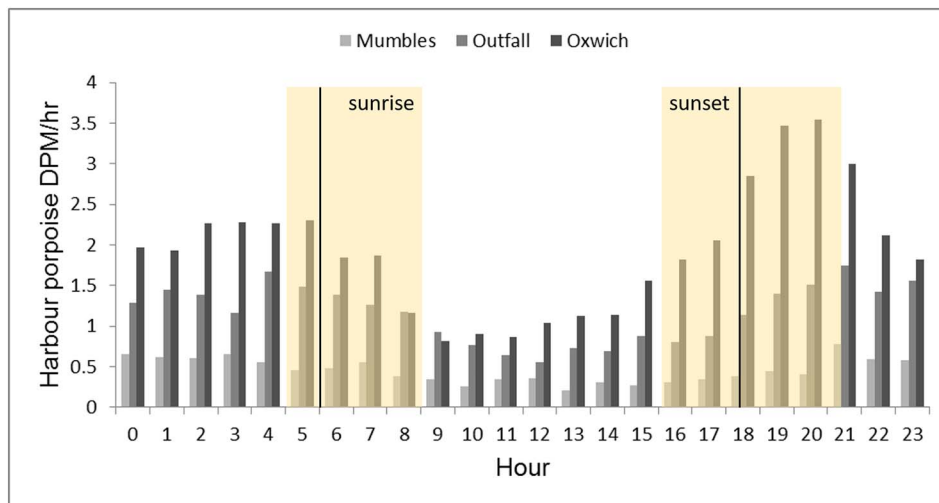


Fig. 6. Mean detection positive minutes (DPM) for harbour porpoise for each hour of the day at each C-POD monitoring location. Yellow bars indicate the annual range of sunrise and sunset times in Swansea Bay, the vertical black lines depict the average time of sunrise and sunset. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

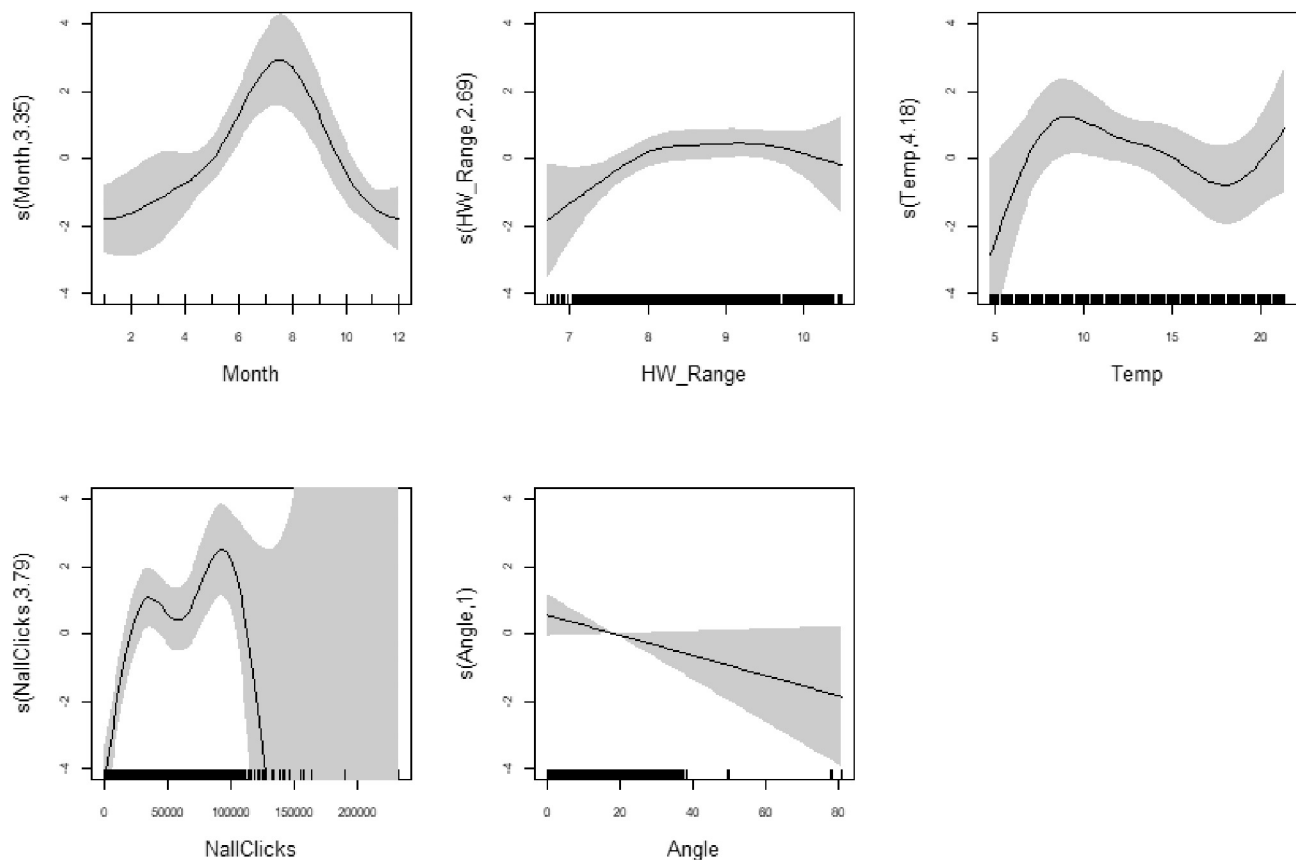


Fig. 7. Fitted relationships for the dolphin detection model based on GAM/BAM standard errors. The grey areas around the relationship are the 95% confidence intervals for each smooth covariate. For factor variables this is represented by dotted lines. The y-axis shows the partial residuals for each model covariate generated by regressing the response on the other covariates.

monitoring locations, although there was considerable variation in detection rates between sites. Highest number of detections were logged consistently at Oxwich Bay.

4.2. Prey species driving porpoise presence

Foraging clicks mirrored the seasonal and diel patterns in overall presence indicating that porpoise spend most of their time feeding in the bay, and that their foraging patterns are greatly influenced by season and time of day. Understanding what prey species the porpoise are targeting can help assess how the porpoise are likely to utilise the

bay during the construction and operational phases of the lagoon. With little or no dietary studies conducted on cetaceans in Welsh waters (Evans and Hinter, 2012), evidence from elsewhere must be used to surmise what porpoise are most likely to be feeding on in the Swansea Bay area. In the North East Atlantic, gadoids (*Trisopterus* sp. including bib *T. luscus*, and poor cod *T. minutus*), sand eels (Ammodytidae) and gobies (Gobiidae), are thought to be the most important prey for porpoises, as well as herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (Borjesson et al., 2003; Santos et al., 2004; Santos and Pierce, 2003; Sveegaard et al., 2012). Studies from the northeast Atlantic have found a shift in predation of largely clupeids to more gadoids and sand eels

since the decline in herring stocks from the 1960s (Santos and Pierce, 2003). Whiting (*Merlangius merlangus*), and sand eels are the most abundant prey items found in stomach contents of stranded animals around Scotland (Santos et al., 2004; Santos and Pierce, 2003).

Long-term data collected at another Bristol Channel site (Severn Estuary by Hinkley Point, Bridgewater) provides evidence of the fish species presence for the estuary and potential prey availability for local cetaceans, with sand goby, whiting and sprat being the three most abundant species (Henderson, 2007; Henderson and Bird, 2010). Yearly fish surveys carried out by Swansea University within Swansea Bay reflect this trend, with observations over the past 8 years recording numerous potential prey species, including high numbers of gobies, whiting and sprat. Other possible prey species such as plaice, sole (*Solea solea*), solenette (*Buglossidium luteum*) and cephalopods (including little cuttle, *Sepiella atlantica*, squid, *Loligo vulgaris* and cuttlefish, *Sepia officinalis*) have also been regularly recorded in Swansea Bay (Horsfall, Garcia de Leaniz, pers. comm. 2017) which could also be contributing to the diet of porpoises foraging in the vicinity. In addition, there is evidence of areas of Swansea Bay being used as spawning grounds by sand eels and sole, and as nursery grounds for herring, plaice (*Pleuronectes platessa*), cod (*Gadus morhua*), whiting, mackerel (*Scomber scombrus*), sole and sand eels (Ellis et al., 2012). Is it likely that the peak in late summer and autumn foraging detections could be due to an increase in abundance of two key prey species; mackerel and herring. Whereas the elevated numbers of foraging detected in winter months could be due to whiting, which spawn earlier in the year (February to June) (Ellis et al., 2012) resulting in higher numbers of juvenile whiting utilizing the bay in winter.

The increase in foraging activity after sunset could indicate preference for nocturnal fish such as plaice and other flatfish. Although a similar diel pattern between the sites was evident, it is likely that the different substrate types in each would affect the types of prey species found there. Without photographic evidence or detailed stranding reports from animals known to have frequented the bay it is not possible to pinpoint which exact prey species drive porpoise presence in the study site. Interestingly the data shows no or negligible effect of tidal cycle on porpoise foraging, probably due to absence of tidally affected foraging sites, such as headlands narrow water flows, where many studies have shown strong sites specific temporal patterns in habitat use linked to a tidal cycle (Pierpoint, 2017; Williamson et al., 2017).

4.3. Dolphin acoustic encounters

The acoustic data confirms visually observations of occasional visits by delphinids in Swansea bay, but the presence was relatively low throughout the sampling period at all locations, and therefore was not considered to have a significant effect on porpoise behaviour (Simon et al., 2010; Nuuttila et al., 2017). Despite the lack of data, some temporal patterns were evident in dolphin detections but the models were not conclusive to warrant a full description on dolphin presence in the area.

As dolphins produce much louder echolocation clicks than porpoises, they can be detected much further away than porpoises, although the longer distance may distort the signal and make it more difficult to distinguish as a dolphin click. Unlike porpoises who have been reported to echolocate a large part of the time making them more available for acoustic detection (Akamatsu et al., 2007), dolphins are not vocal all the time, and produce sounds other than clicks when socialising and resting, which make them difficult to detect with C-PODs. It is therefore likely that some detections were missed and that others originated from dolphins travelling or foraging further offshore, as often witnessed by local fishermen. Although not a key concern for a MRE development, this data shows that some species of dolphins do occasionally visit Swansea Bay, particularly in the summer months, and as we detect their echolocation clicks, we can imply that these transient visitors are probably feeding in the area.

4.4. Potential impact of a tidal lagoon in Swansea Bay - displacement

Constructing the tidal lagoon will enclose a large part of the inner Swansea Bay and make this area unavailable for cetaceans. A considerable part of this will be shallow intertidal mud and sand, habitat not frequented by cetaceans. At the deeper end of the lagoon footprint, the current sewage outfall site seems to be a habitat preferred by porpoises, probably due to increased prey availability benefitting from nutrient concentrations in its vicinity. The Swansea Bay Tidal Lagoon's future plans are to extend this outfall pipe approximately 1 km outside of the Lagoon structure, possibly creating an equally attractive habitat for porpoises and their prey. During the construction phase, increased noise and vessel presence are likely to deter cetaceans from frequenting the area, but this may be temporary as shown in studies of windfarm builds in the North Sea (Mann and Teilmann, 2013; Scheidat et al., 2011). A recent report from Scottish Natural Heritage based on data from grid-connected tidal and wave test sites at the European Marine Energy Centre (EMEC) in Orkney, found that there was no long-term displacement effects to bird or marine mammal populations from these devices and that main negative effect comes from initial infrastructure installations, indicating that it may not be the physical presence of the device or its infrastructure that is causing this change in density, but rather the increased vessel movements that are associated with installation activities (Long, 2017). Immediate effects of pile-driving on harbour porpoises from windfarm studies are well known (Dähne et al., 2013) but long-term consequences are more difficult to assess. The report by Long underlines the fact that despite extensive datasets, in many cases it has not been possible to discern change in abundance or animal activity, due to inappropriate survey design and the large natural fluctuations in bird and cetacean abundance and habitat use from year to year.

If disruption from the structure of the lagoon and operational noise from the turbines can be mitigated against, it may be possible that porpoises deterred from the area during construction will return. However, this will be dependent upon whether their prey species are able to inhabit the seabed surrounding the lagoon. Should this not be the case, the porpoise, being opportunistic feeders, will most likely choose to forage elsewhere to meet their high energetic demands (Wisniewska et al., 2016). Although Swansea Bay has not been designated a porpoise protected SAC, porpoises do in fact use the Bay all year round, and when detected, an average of 78% of their vocalisations across the three study sites can be assigned to foraging. It would therefore prudent to mitigate the worst impact from construction by avoiding working close to sunset and night time during the late summer and early autumn periods, when porpoise foraging detections were found to be highest.

4.5. Collision risk

There have been some concerns that the proposed tidal lagoon underwater turbines will pose a serious risk to cetaceans in Swansea Bay if the animals swim into and collide with the turbines (Wilson et al., 2007). As the turbines are part of a wall structure rather than exposed turbine blades in open water, the risk is probably considerably lower than those of typical tidal stream devices (Khan et al., 2009). It is currently not known how porpoises will react to the lagoon structure, its construction and operation. Due to their excellent echolocation and target discrimination abilities (Au et al., 2017; Villadsgaard et al., 2007) cetaceans are typically able to avoid collision with marine structures such as stationary nets, harbours and break walls, although they will forage close to such structures if these provide beneficial habitat for their prey. Without the lagoon structure in place and without fully understanding the size of the population and what proportion of individuals use the bay it is very difficult to assess the extent of impact of the development. In Scotland, the policy of 'survey, deploy and monitor' has enabled regulators and the industry to assess

environmental impacts of wave and tidal energy devices and considerably increased the understanding of effects of novel MRE devices and consequently enabled a more informed decision making and consenting process (Marine Scotland, 2016). Assessing collision risk or potential displacement in Swansea Bay is difficult due to lack of baseline data but it is likely that considering the number of turbines and the large scale of the deployment, a thorough survey and monitoring protocol and a mitigation system for collision risk through adaptive management strategies will most likely be required by the regulator. An acoustic and visual monitoring regime of the operational turbines will reveal any actual or potential collisions, as well as any avoidance behaviour and this data can be used to design the most effective way to deter animals from entering the vicinity of the turbines if necessary (Wilson and Carter, 2013).

4.6. Considerations for acoustic studies

Acoustic monitoring is not without its challenges, one of which is the risk of equipment or data loss due to environmental hazards such as storms and currents, but also due to anthropogenic activities, such as shipping, dredging and trawling. The C-POD records the overall click levels (NAIIClicks) as well as the angle of the logger from vertical, and these can be used to assess the level of ambient noise and the position of the logger in the water column. Periods when the logger is not vertical as well as those with excessive noise can easily be deleted from the data before analysis. Here the variable all clicks was a significant predictor of porpoise detections; initial increase in all clicks logged also resulted in increase of porpoise clicks. However, after a certain threshold this effect would plateau off or begin to fluctuate. The position of the C-POD in the water did not have an effect on foraging clicks and only minor effect on porpoise detections. It did have a significant effect on dolphin detection, although the model results were somewhat inconclusive, probably due to lack of data overall.

In this study, difficulties arose in deploying devices off Scarweather sandbanks due to winter storms, and another two devices were lost due to high shipping activity in the middle of the Bay. This, combined with the issues experienced with acoustic releases, means that gaps in data collection were inevitable. Only few days of recordings in December and January were achieved at Scarweather. Although the data shows high levels of porpoise activity, the lack of deployment coverage at this site was too great and all data from Scarweather was omitted from the analysis. For a better understanding of porpoise activity in Swansea Bay and surrounding area further data collection at this site is recommended. A further consideration for SAM use is the requirement to assess the detection probability of the target species at the selected site. This is affected by physical characteristics of the seabed, water depth, current speed, tidal flow and ambient noise as well as factors that may deter or attract animals to the site such as shipping, vicinity of other structures and of course prey availability (Brandt et al., 2011; Scheidat et al., 2011). We know from experimental studies that the effective detection range of the C-PODs for porpoises in shallow coastal areas varies between approximately 100–450 m (Benjamins et al., 2017; Nuuttila, 2012). The actual area sampled is therefore rather small but the sites used in this study were selected to maximise acoustic encounters, where local fishermen, wildlife watchers and other sea users report frequent sightings of porpoises. To accurately capture the fine-scale patterns in habitat use, many more dataloggers should be deployed across the entire study site and a variety of physical features within it, although this is rarely possible due to financial limitations of most research projects.

4.7. Positive effects of MRE structures

Well planned MRE structures have potential for increasing biodiversity and restoration of depleted sea areas. In Swansea Bay the company (Tidal Lagoon Swansea Bay Plc.) has plans to enhance the

value of this development for biodiversity by creating an artificial reef on the outer structure of the lagoon wall (Callaway et al., 2014). This would include using specially designed building materials to attract colonising animals and plants which in turn will in turn attract crustaceans and fish. Other plans to maintain and increase the bay's biodiversity include restoration of native oyster reefs (*Ostrea edulis*), safeguarding *Sabellaria* reefs and creating seagrass (*Zostera* sp.) meadows within the lagoon itself. Ideally, MRE structures such as the Lagoon would not only provide fossil free energy but would also increase local biodiversity, including prey for cetaceans, whilst simultaneously repelling cetaceans and fish from the vicinity of the turbines to avoid risk from collision.

4.8. Conclusion

Understanding detailed patterns in harbour porpoise habitat use will assist in management and mitigation of anthropogenic disturbance where the species occurs. This is particularly important as tidal energy sites often overlap with areas frequented by porpoises, and there is an ever pressing need to harness more renewable energy to combat climate change. Static acoustic monitoring devices can provide a practical and cost-effective method to gather long term data to discern fine scale temporal changes required to effectively assess impacts from MRE and other coastal developments. They can also reveal patterns in fine scale spatial heterogeneity, if an array of multiple devices can be used to cover an entire area of interest. In areas with very high tidal flow this can be impractical and lead to data or equipment losses, however, in some sites, the loggers can be placed just outside the main flow areas and still gather important information on habitat use and animal travel across the proposed development site. By lowering the constraints of limited fine scale data, developers are better able to understand and avoid times and areas where impact is likely to be at its highest, and mitigate negative effects on cetacean populations already under stress from various cumulative anthropogenic pressures.

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Appendix A. Supplementary data

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References

- Akamatsu, T., Teilmann, J., Miller, L.A., Tougaard, J., Dietz, R., Wang, D., Wang, K., Siebert, U., Naito, Y., 2007. Comparison of echolocation behaviour between coastal and riverine porpoises. *Deep-Sea Res. II Top. Stud. Oceanogr.* 54, 520–526. <http://dx.doi.org/10.1109/UT.2007.370755>.
- Au, W.W., Fay, R.R., 2000. *Hearing by Whales and Dolphins*. Springer-Verlag, New York, Berlin, Heidelberg.
- Au, W.W.L., Hastings, M.C., 2008. *Principles of Marine Bioacoustics*. Springer Science + Business Media, LLC, New York. <http://dx.doi.org/10.1007/978-0-387-78365-9>.
- Au, W.W.L., Floyd, R.W., Penner, R.H., Murchison, A.E., 1974. Measurement of echolocation signals of the Atlantic bottlenose dolphin, *Tursiops truncatus* Montagu, in open waters. *J. Acoust. Soc. Am.* 56, 1280. <https://doi.org/10.1121/1.1903419>.
- Au, W.W.L., Kastelein, R.A., Tineke, R., Schooneman, N.M., 1999. Transmission beam pattern and echolocation signals of a harbor porpoise (*Phocoena phocoena*). *J. Acoust. Soc. Am.* 106, 3699–3705.
- Au, W.W.L., Atkins, J., Harley, H.E., Volpillier, H., Fellner, W., 2017. The dynamics of a dolphin's biosonar signals while performing target discrimination tasks. *J. Acoust.*

- Soc. Am. 141, 3486. <http://dx.doi.org/10.1121/1.4987267>.
- Baines, M.E., Evans, P.G.H., 2012. Atlas of the Marine Mammals of Wales, 2nd edition. CCW Monitoring Report No. 68.
- Bell, C., 2016. POLTIPS.3. Applications Team at the National Oceanographic Centre.
- Benjamins, S., van Geel, N., Hastie, G., Elliott, J., Wilson, B., 2017. Harbour porpoise distribution can vary at small spatiotemporal scales in energetic habitats. *Deep-Sea Res. II* 141, 191–202. <http://dx.doi.org/10.1016/j.dsr2.2016.07.002>.
- Benke, H., Bräger, S., Dähne, M., Gallus, A., Hansen, S., Honnef, C.G., Jabbusch, M., Koblit, J.C., Krügel, K., Liebschner, A., Narberhaus, I., Verfuß, U.K., 2014. Baltic Sea harbour porpoise populations: status and conservation needs derived from recent survey results. *Mar. Ecol. Prog. Ser.* 495, 275–290. <http://dx.doi.org/10.3354/meps10538>.
- Berrow, S., Brien, J.O., Connor, I.O., McGrath, D., Berrow, S., Brien, J.O., Connor, I.O., McGrath, D., 2009. Abundance estimate and acoustic monitoring of harbour porpoises (*Phocoena phocoena*) in the Basket Islands' candidate Special Area of Conservation. In: *Biology and Environment: Proceedings of the Royal Irish Academy*, pp. 35–46. <http://dx.doi.org/10.3318/BIOE.2009.109.1.35>.
- Borjesson, P., Berggren, P., Ganning, B., 2003. Diet of harbor porpoises in the Kattegat and Skagerrak seas: accounting for individual variation and sample size. *Mar. Mamm. Sci.* 19, 38–58.
- Brandt, M.J., Diederichs, A., Betke, K., Nehls, G., 2011. Responses of harbour porpoises to pile driving at the Horns Rev II offshore wind farm in the Danish North Sea. *Mar. Ecol. Prog. Ser.* 421, 205–216. <http://dx.doi.org/10.3354/meps08888>.
- Brandt, M.J., Hansen, S., Diederichs, A., Nehls, G., 2014. Do man-made structures and water depth affect the diel rhythms in click recordings of harbor porpoises (*Phocoena phocoena*)? *Mar. Mamm. Sci.* 30, 1109–1121. <http://dx.doi.org/10.1111/mms.12112>.
- Brookes, K.L., Bailey, H., Thompson, P.M., 2013. Predictions from harbor porpoise habitat association models are confirmed by long-term passive acoustic monitoring. *J. Acoust. Soc. Am.* 134. <http://dx.doi.org/10.1121/1.4816577>.
- Callaway, R., 2016. Historical data reveal 30-year persistence of benthic Fauna associations in heavily modified waterbody. *Front. Mar. Sci.* 3. <http://dx.doi.org/10.3389/fmars.2016.00141>.
- Callaway, R., Lock, G., Bishop, E., Blazey, T., Unsworth, R., Bertelli, C.M., 2014. Tidal energy lagoon in Swansea Bay enhancing its value for biodiversity by creating an artificial reef. In: *Poster Presented at 2014 Conference on Environmental Interactions of Marine Renewable Energies (EIMR) in Stornoway, UK*.
- Carlstrom, J., 2005. Diel variation in echolocation behavior of wild harbor porpoises. *Mar. Mamm. Sci.* 21, 1–12. <http://dx.doi.org/10.1111/j.1748-7692.2005.tb01204.x>.
- Carstensen, J., Henriksen, O.D., Teilmann, J., 2006. Impacts of offshore wind farm construction on harbour porpoises: acoustic monitoring of echolocation activity using porpoise detectors (T-PODs). *Mar. Ecol. Prog. Ser.* 321, 295–308. <http://dx.doi.org/10.3354/meps321295>.
- Cox, T.M., Read, A.J., Solow, A., Tregenza, N., 2001. Will harbour porpoises (*Phocoena phocoena*) habituate to pingers? *J. Cetacean Res. Manag.* 3, 81–86.
- Dähne, M., Gilles, A., Lucke, K., Peschko, V., Adler, S., Krügel, K., Sundermeyer, J., Siebert, U., 2013. Effects of pile-driving on harbour porpoises (*Phocoena phocoena*) at the first offshore wind farm in Germany. *Environ. Res. Lett.* 8. <http://dx.doi.org/10.1088/1748-9326/8/2/025002>. (16 pp.).
- Davies, C.M., 1974. Variability of sediment suspended in rotatory currents, Swansea Bay (Bristol Channel), Great Britain. *Mar. Geol.* 16, M31–M38. [http://dx.doi.org/10.1016/0025-3227\(74\)90055-3](http://dx.doi.org/10.1016/0025-3227(74)90055-3).
- Dolman, S., Simmonds, M., 2010. Towards best environmental practice for cetacean conservation in developing Scotland's marine renewable energy. *Mar. Policy* 34, 1021–1027. <http://dx.doi.org/10.1016/j.marpol.2010.02.009>.
- Ellis, J.R., Milligan, S.P., Readdy, L., Taylor, N., Brown, M.J., 2012. Spawning and Nursery Grounds of Selected Fish Species in UK Waters. Lowestoft.
- Embling, C.B., Gillibrand, P.A., Gordon, J., Shrimpton, J., Stevick, P.T., Hammond, P.S., 2010. Using habitat models to identify suitable sites for marine protected areas for harbour porpoises (*Phocoena phocoena*). *Biol. Conserv.* 143, 267–279. <http://dx.doi.org/10.1016/j.biocon.2009.09.005>.
- Evans, P.G.H., 2012. Recommended Management Units for Marine Mammals in Welsh Waters. CCW Policy Research Report No. 12/1.
- Evans, P.G.H., Hammond, P.S., 2004. Monitoring cetaceans in European waters. *Mammal Rev.* 34, 131–156. <http://dx.doi.org/10.1046/j.0305-1838.2003.00027.x>.
- Evans, P.G.H., Hinder, K., 2012. A Review of the Direct and Indirect Impacts of Fishing Activities on Marine Mammals in Welsh Waters. CCW Policy Research Report No. 12/5. pp. 1–172.
- Henderson, P.A., 2007. Discrete and continuous change in the fish community of the Bristol Channel in response to climate change. *J. Mar. Biol. Assoc. UK* 87, 589–598. <http://dx.doi.org/10.1017/S0025315407052447>.
- Henderson, P.A., Bird, D.J., 2010. Fish and macro-crustacean communities and their dynamics in the Severn Estuary. *Mar. Pollut. Bull.* 61, 100–114. <http://dx.doi.org/10.1016/j.marpolbul.2009.12.017>.
- JNCC, 2016. Harbour Porpoise (*Phocoena phocoena*) Possible Special Area of Conservation: Bristol Channel Approaches/Dynesfeydd Môr Hafren Draft Conservation Objectives and Advice on Activities.
- Khan, M.J., Bhuyan, G., Iqbal, M.T., Quaique, J.E., 2009. Hydrokinetic energy conversion systems and assessment of horizontal and vertical axis turbines for river and tidal applications: a technology status review. *Appl. Energy* 86, 1823–1835. <http://dx.doi.org/10.1016/j.apenergy.2009.02.017>.
- Linnenschmidt, M., Teilmann, J., Akamatsu, T., Dietz, R., Miller, L.A., 2013. Biosonar, dive, and foraging activity of satellite tracked harbor porpoises (*Phocoena phocoena*). *Mar. Mamm. Sci.* 29, 77–97. <http://dx.doi.org/10.1111/j.1748-7692.2012.00592.x>.
- Long, C., 2017. Analysis of the Possible Displacement of Bird and Marine Mammal Species Related to the Installation and Operation of Marine Energy Conversion Systems. Natural Heritage Commissioned Report No. 947.
- Manasseh, R., Sannasiraj, S.A., McInnes, K.L., Sundar, V., Jaliha, P., 2017. Integration of wave energy and other marine renewable energy sources with the needs of coastal societies. *Int. J. Ocean Clim. Syst.* 8, 19–36. <http://dx.doi.org/10.1177/1759313116683962>.
- Mann, J., Teilmann, J., 2013. Environmental impact of wind energy. *Environ. Res. Lett.* 8. <http://dx.doi.org/10.1088/1748-9326/8/3/035001>.
- Marine Scotland, 2016. Survey, deploy and monitor licensing policy guidance. <http://www.gov.scot/Topics/marine/Licensing/marine/Applications/SDM>.
- Mikkelsen, L., Mouritsen, K.N., Dahl, K., Teilmann, J., Tougaard, J., 2013. Re-established stony reef attracts harbour porpoises *Phocoena phocoena*. *Mar. Ecol. Prog. Ser.* 481, 239–248. <http://dx.doi.org/10.3354/meps10260>.
- Murtaugh, P.A., 2014. In defense of P values. *Ecology* 95 (3), 611–617.
- Nuuttila, H.K., 2012. Static Acoustic Monitoring of Cetaceans in Cardigan Bay, Wales. Bangor.
- Nuuttila, H.K., Hiddink, J.G., Meier, R., Turner, J.R., Bennell, J.D., Evans, P.G.H., 2013a. Acoustic detection probability of bottlenose dolphins, *Tursiops truncatus*, with static acoustic dataloggers in Cardigan Bay, Wales. *J. Acoust. Soc. Am.* 2596–2609. <http://dx.doi.org/10.1121/1.4816586>.
- Nuuttila, H.K., Meier, R., Evans, P.G.H., Turner, J.R., Bennell, J.D., Hiddink, J.G., 2013b. Identifying foraging behaviour of wild bottlenose dolphins (*Tursiops truncatus*) and harbour porpoises (*Phocoena phocoena*) with static acoustic dataloggers. *Aquat. Mamm.* 39, 147–161. <http://dx.doi.org/10.1578/AM.39.2.2013.147>.
- Nuuttila, H.K., Courteney-Jones, W., Baulch, S., Simon, M., Evans, P.G.H., 2017. Don't forget the porpoise: acoustic monitoring reveals fine scale temporal variation between bottlenose dolphin and harbour porpoise in Cardigan Bay SAC. *Mar. Biol.* 164, 50. <http://dx.doi.org/10.1007/s00227-017-3081-5>.
- Philpott, E., Englund, A., Ingram, S., Rogan, E., 2017. Using T-PODs to investigate the echolocation of coastal bottlenose dolphins. *J. Mar. Biol. Assoc. UK* 87, 11–17. <http://dx.doi.org/10.1017/S002531540705494X>.
- Pierpoint, C., 2017. Harbour porpoise (*Phocoena phocoena*) foraging strategy at a high energy, near-shore site in south-west Wales, UK. *J. Mar. Biol. Assoc. UK* 88, 1167–1173. <http://dx.doi.org/10.1017/S0025315408000507>.
- Pirotta, E., Thompson, P.M., Miller, P.I., Brookes, K.L., Cheney, B., Barton, T.R., Graham, I.M., Lusseau, D., 2014. Scale-dependent Foraging Ecology of a Marine Top Predator Modelled Using Passive Acoustic Data. pp. 206–217. <http://dx.doi.org/10.1111/1365-2435.12146>.
- Pye, K., Blott, S.J., 2014. Estuarine, coastal and shelf science the geomorphology of UK estuaries: the role of geological controls, antecedent conditions and human activities. *Estuar. Coast. Shelf Sci.* 150, 196–214. <http://dx.doi.org/10.1016/j.ecss.2014.05.014>.
- Rayment, W., Dawson, S.M., 2009. Trialling an automated passive acoustic detector (T-POD) with Hector's dolphins (*Cephalorhynchus hectori*). *J. Mar. Biol. Assoc. UK* 89, 1015–1022. <http://dx.doi.org/10.1017/S0025315409003129>.
- Reid, J.B., Evans, P.G.H., Northridge, S.P., 2003. Atlas of Cetacean Distribution in North-West European Waters. Joint Nature Conservation Committee, Peterborough.
- Santos, M.B., Pierce, G.J., 2003. The diet of harbor porpoises (*Phocoena phocoena*) in the Northeast Atlantic. *Oceanogr. Mar. Biol.* 355–390.
- Santos, M.B., Pierce, G.J., Learmouth, J.A., 2004. Variability in the diet of harbor porpoises (*Phocoena phocoena*) in Scottish waters 1992–2003. *Mar. Mamm. Sci.* 20, 1–27.
- Schaffel, T., Bräger, S., Gallus, A., Dähne, M., Krügel, K., Herrmann, A., Jabbusch, M., Ruf, T., Verfuß, U.K., Benke, H., Koblit, J.C., 2016. Diel and seasonal patterns in acoustic presence and foraging behaviour of free-ranging harbour porpoises. *Mar. Ecol. Prog. Ser.* 547, 257–272. <http://dx.doi.org/10.3354/meps11627>.
- Scheidat, M., Tougaard, J., Brasseur, S., Carstensen, J., van Polanen, T.P., Teilmann, J., Peter, R., 2011. Harbour porpoises (*Phocoena phocoena*) and wind farms: a case study in the Dutch North Sea. *Environ. Res. Lett.* 6. <http://dx.doi.org/10.1088/1748-9326/6/2/025102>.
- Simmonds, M.P., Brown, V.C., 2010. Is there a conflict between cetacean conservation and marine renewable-energy developments? *Wildl. Res.* 37.
- Simon, M., Nuuttila, H., Reyes-Zamudio, M.M., Ugarte, F., Verfuß, U., Evans, P.G.H., 2010. Passive acoustic monitoring of bottlenose dolphin and harbour porpoise, in Cardigan Bay, Wales, with implications for habitat use and partitioning. *J. Mar. Biol. Assoc. UK* 90, 1539–1545. <http://dx.doi.org/10.1108/17506200710779521>.
- Sveegaard, S., Andreasen, H., Mouritsen, K.N., Peder, J., Jonas, J., Carl, T., 2012. Correlation between the seasonal distribution of harbour porpoises and their prey in the Sound, Baltic Sea. *Mar. Biol.* 159, 1029–1037. <http://dx.doi.org/10.1007/s00227-012-1883-z>.
- Teilmann, J., Carstensen, J., 2012. Negative long term effects on harbour porpoises from a large scale offshore wind farm in the Baltic — evidence of slow recovery. *Environ. Res. Lett.* 7. <http://dx.doi.org/10.1088/1748-9326/7/4/045101>. (10 pp.).
- Teilmann, J., Miller, L.A., Kirketerp, T., Kastelein, R.A., Madsen, P.T., Nielsen, B.K., Au, W.W.L., 2002. Characteristics of echolocation signals used by a harbour porpoise (*Phocoena phocoena*) in target detection experiment. *Aquat. Mamm.* 28.3 (28), 275–284.
- Thompson, P.M., Brookes, K.L., Cordes, L.S., 2015. Integrating passive acoustic and visual data to model spatial patterns of occurrence in coastal dolphins. *ICES J. Mar. Sci.* 72, 651–660 (doi:10.1093).
- Todd, V.L.G., Pearce, W.D., Tregenza, N.C., Lepper, P.A., Todd, I.B., Diel, I.B., 2009. Diel echolocation activity of harbour porpoises (*Phocoena phocoena*) around North Sea offshore gas installations. *ICES J. Mar. Sci.* 66, 734–745.
- Tregenza, N., 2014. CPD.exe: guide for users. <http://www.cheloniac.co.uk/downloads/CPD.pdf>.
- van Rij, J., Wieling, M., Baayen, R., van Rijn, H., 2016. "itsadug: Interpreting Time Series and Autocorrelated Data Using GAMMs." R Package Version 2.2.
- Verfuß, U.K., Honnef, C.G., Mending, A., Dähne, M., Mundry, R., Benke, H., 2007.

- Seasonal and geographical variation of harbour porpoise (*Phocoena phocoena*) habitat use in the German Baltic Sea monitored by passive acoustic methods (PODs). *J. Mar. Biol. Assoc. UK* 87, 165–176. <http://dx.doi.org/10.1007/3-540-33291-X.13>.
- Verfuß, U.K., Miller, L.A., Pilz, P.K.D., Schnitzler, H., 2009. Echolocation by two foraging harbour porpoises (*Phocoena phocoena*). *J. Exp. Biol.* 212, 823–834. <http://dx.doi.org/10.1242/jeb.022137>.
- Villadsgaard, A., Wahlberg, M., Tougaard, J., 2007. Echolocation signals of wild harbour porpoises, *Phocoena phocoena*. *J. Exp. Biol.* 210, 56–64. <http://dx.doi.org/10.1242/jeb.02618>.
- Wahlberg, M., Jensen, F.H., Soto, N.A., Beedholm, K., Bejder, L., Oliveira, C., Rasmussen, M., Simon, M., Villadsgaard, A., Madsen, P.T., 2011. Source parameters of echolocation clicks from wild bottlenose dolphins (*Tursiops aduncus* and *Tursiops truncatus*). *J. Acoust. Soc. Am.* 130. <http://dx.doi.org/10.1121/1.3624822>.
- Watkins, H., Colley, R., 2004. Harbour Porpoise *Phocoena phocoena* Occurrence Carmarthen Bay - Gower Peninsula - Swansea Bay.
- Williamson, L.D., Brookes, K.L., Scott, B.E., Graham, I.M., Bradbury, G., Hammond, P.S., Thompson, P.M., 2016. Echolocation detections and digital video surveys provide reliable estimates of the relative density of harbour porpoises. *Methods Ecol. Evol.* 7, 762–769. <http://dx.doi.org/10.1111/2041-210X.12538>.
- Williamson, L.D., Brookes, K.L., Scott, B.E., Graham, I.M., Thompson, P.M., 2017. Diurnal variation in harbour porpoise detection — potential implications for management. *Mar. Ecol. Prog. Ser.* 570, 223–232. <http://dx.doi.org/10.3354/meps12118>.
- Wilson, B., Carter, C., 2013. The Use of Acoustic Devices to Warn Marine Mammals of Tidal-Stream Energy Devices. Report Prepared for Marine Scotland, Scottish Government.
- Wilson, B., Batty, R.S., Daunt, F., Carter, C., 2007. Collision Risks between Marine Renewable Energy Devices and Mammals, Fish and Diving Birds. Report to the Scottish Executive.
- Wisniewska, D.M., Johnson, M., Teilmann, J., Miller, L.A., Siebert, U., Shearer, J., 2016. Ultra-high Foraging Rates of Harbor Porpoises Make Them Vulnerable to Anthropogenic Disturbance Report Ultra-high Foraging Rates of Harbor Porpoises Make Them Vulnerable to Anthropogenic Disturbance. pp. 1–6. <http://dx.doi.org/10.1016/j.cub.2016.03.069>.
- Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc.* 73, 3–36.
- Wood, S.N., Goude, Y., Shaw, S., 2015. Generalized additive models for large data sets. *J. R. Stat. Soc.* 64, 139–155.