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Harbour porpoise distribution can vary at small spatiotemporal scales in energetic habitats

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ABSTRACT

Marine habitat heterogeneity underpins species distribution and can be generated through interactions between physical and biological drivers at multiple spatiotemporal scales. Passive acoustic monitoring (PAM) is used worldwide to study potential impacts of marine industrial activities on cetaceans, but understanding of animals' site use at small spatiotemporal scales (< 1 km, < 1 day) remains limited. Small-scale variability in vocalising harbour porpoise (*Phocoena phocoena*) distribution within two Scottish marine renewable energy development (MRED) sites was investigated by deploying dense arrays of C-POD passive acoustic detectors at a wave energy test site (the European Marine Energy Centre [Billia Croo, Orkney]) and by a minor tidal-stream site (Scarba [Inner Hebrides]). Respective arrays consisted of 7 and 11 moorings containing two C-PODs each and were deployed for up to 55 days. Minimum inter-mooring distances varied between $\sim$300–600 m. All C-POD data were analysed at a temporal resolution of whole minutes, with each minute classified as 1 or 0 on the basis of presence/absence of porpoise click trains (Porpoise-Positive Minutes/PPMs). Porpoise detection rates were analysed using Generalised Additive Models (GAMs) with Generalised Estimation Equations (GEEs).

Although there were many porpoise detections (wave test site: $N=3,432$; tidal-stream site: $N=17,366$), daily detection rates varied significantly within both arrays. Within the wave site array (< 1 km diameter), average daily detection rates varied from 4.3 to 14.8 PPMs/day. Within the tidal-stream array (< 2 km diameter), average daily detection rates varied from 10.3 to 49.7 PPMs/day. GAM-GEE model results for individual moorings within both arrays indicated linkages between porpoise presence and small-scale heterogeneity among different environmental covariates (e.g., tidal phase, time of day). Porpoise detection rates varied considerably but with coherent patterns between moorings only several hundred metres apart and within hours. These patterns presumably have ecological relevance.

These results indicate that, in energetically active and heterogeneous areas, porpoises can display significant spatiotemporal variability in site use at scales of hundreds of metres and hours. Such variability will not be identified when using solitary moored PAM detectors (a common practice for site-based cetacean monitoring), but may be highly relevant for site-based impact assessments of MRED and other coastal developments. PAM arrays encompassing several detectors spread across a site therefore appear to be a more appropriate tool to study site-specific cetacean use of spatiotemporally heterogeneous habitat and assess the potential impacts of coastal and nearshore developments at small scales.

1. Introduction

Marine habitat heterogeneity is recognised as a crucial driver of species distribution and wider ecosystem structure (Barry and Dayton, 1991) and can be generated through interactions between physical and biological drivers at multiple spatiotemporal scales (García-Charton et al., 2004; Connell, 2005; Buhl-Mortensen et al., 2010). Many anthropogenic activities in the marine environment pose risks to species and ecosystems, and monitoring these activities to assess the probability, magnitude and mechanisms of their impacts on the receiving environment is a requirement under many regulatory frameworks (e.g., EU Habitats Directive and Marine Strategy Framework Directive, US FDA legislation, Australian Environment Protection and Biodiversity Conservation Act 1999). Efforts to gather appropriate data to assess these impacts have greatly increased over the past decades (Carstensen et al., 2006; Carstensen, 2014). With increasing data needs, however, it becomes increasingly important to ensure that data

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collection efforts are undertaken at spatiotemporal scales appropriate to answering management questions and capturing relevant habitat heterogeneity (Wiens, 1989; De Jonge et al., 2006; Tett et al., 2013). Every monitoring programme represents a compromise between improved data resolution and practical limitations (e.g., financial resources, logistical difficulties; Franco et al., 2015).

Cetaceans are often the subject of considerable monitoring efforts due to their conservation status and high public profile (Macleod et al., 2011). Monitoring programmes often focus on assessing cetacean distribution, abundance and habitat use, to determine overlap with, and degree of impact by, anthropogenic activities at particular development sites that are typically ∼10 to several 100 km² in size (Sparling et al., 2015). Such programmes are typically associated with site-specific activities (e.g., oil and gas extraction, marine renewable energy generation, coastal development) and therefore conducted across spatially discrete areas (often < 100 km²). Cetaceans' extensive distribution and capacity for rapid movements across sites often complicate attempts to develop monitoring programmes capable of generating information at ecologically relevant scales. Individual site-based monitoring programmes are poorly suited to study mobile animals at very large scales (100–1000 km, decades; Macleod et al., 2011), but may also struggle to capture fine-scale variability in distribution and habitat use (< 1 km, hours) unless specifically designed to that effect. High-resolution data can be gathered through visual observation (e.g., De Boer et al., 2014), equipping animals with telemetry tags (e.g., Johnston et al., 2005) or passive acoustic monitoring methods (PAM; e.g., Tyack et al., 2011); however, all of these methods require considerable effort to obtain sufficient observations for robust assessment of status and/or risk. For this reason, studies often undertake monitoring at a limited number of locations (often at a single location) within a site. Risks are generally assessed on the basis of an interpolated or assumed uniform density or distribution of animals across the site (Wilson et al., 2006), but this approach may not be appropriate if there is high spatiotemporal heterogeneity in animal distribution (Sheaves, 2006; Sparling et al., 2015).

Harbour porpoises (Phocoena phocoena) are small odontocete cetaceans with a circumpolar distribution in cold-temperate waters of the Northern Hemisphere (Gaskin, 1984). Porpoises are highly vocal, producing stereotyped vocalisations allowing for the use of PAM as a tool to study potential impacts of anthropogenic activities (e.g., Brandt et al., 2011; Gallus et al., 2012). Numerous studies have described fine-scale (∼1–10 km²) and mesoscale (10–100 s of km²) variability in porpoise presence (Read and Westgate, 1997; Verfuß et al., 2007; Mikkelsen et al., 2013), but high-resolution information of their habitat use at very small spatiotemporal scales (≤1 km², hours) remains limited (Johnston et al., 2005; Isojunno et al., 2012; Jones et al., 2014). Mobile PAM surveys using towed hydrophone arrays can provide wide spatial coverage, but cannot easily resolve temporal variability. In contrast, individual moored passive acoustic detectors can provide high-temporal resolution data over long periods at discrete locations, but effective detection radii are typically limited (Kyhn et al., 2008, 2012). Detection ranges of PAM detectors are also negatively impacted by high ambient noise levels, such as might occur during storms (through breaking waves; Hildebrand, 2009) or during peak tidal flows (Tonolla et al., 2010; Carter, 2013).The assumption that data from sparse fixed PAM efforts, or even solitary PAM sensors, adequately describe ecologically relevant variability in harbour porpoise distribution and habitat use across a development site remains largely untested.

The present study combines observations from studies at two separate, and contrasting, energetic sites in Scotland, UK (exposed to waves and tidal currents, respectively). Both studies used relatively dense arrays of moored passive acoustic detectors to assess use by harbour porpoise of sites suitable for marine renewable energy development (MRED; Benjamins et al., 2015). The aims of the present study were to assess the significance of spatiotemporal variability in detection rates of echolocating harbour porpoises at small (< 1 km², within hours) scales across both sites and in relation to local environmental variables.

2. Methods

Data were collected using autonomous passive acoustic detectors (C-PODs; Chelonia Ltd., 2015). These are automated, passive acoustic monitoring systems that detect vocalising porpoises, dolphins and other toothed whales by detecting and classifying echolocation click trains (e.g., Castellote et al., 2013; Dähne et al., 2013; Roberts and Read, 2015). They are increasingly used to study harbour porpoises and other echolocating cetaceans at MRED sites (Tollit et al., 2011; Witt et al., 2012; Wilson et al., 2013). C-PODs were all of comparable age and build, and their response to artificial porpoise clicks was tested prior to deployment using an omnidirectional harbour porpoise click train synthesiser (PALv1, producing click trains with a centre frequency of 133 ± 0.5 kHz and source levels of 154 ± 2 dB; F^3 Engineering) at known distances from C-PODs, confirming low inter-device variability. Occasionally, under high ambient noise conditions, C-PODs temporarily stop logging when reaching a pre-set buffer limit of 4,096 clicks, until the start of the next minute. The proportion of each minute thus lost was used as a crude proxy of ambient noise levels. C-PODs also contained an onboard tilt sensor, recording their deflection from vertical (0°=vertical and 90°=horizontal). C-PODs were deployed in arrays in two locations (see below) to capture small-scale heterogeneity in detection rates. Standard moorings consisted of a single rope attached to a weight and float. Two C-PODs were attached to each mooring for purposes of redundancy. In all but one case (see below), C-PODs were deployed near the seabed. C-POD detection ranges depend on ambient noise conditions, but are often considered to be on the order of ∼200–300 m for harbour porpoise echolocation clicks under typical conditions (Kyhn et al., 2008, 2012). Based on previous experiments at Billia Croo using the aforementioned PALv1 click train synthesiser at known distances from C-PODs (Benjamins et al. unpublished data), detection ranges at this exposed site appeared to be < 150 m. To minimise the potential for the same echolocation event to be detected by multiple C-PODs, all inter-mooring distances were kept to 300 m or greater.

2.1. Deployment: Wave energy site

Billia Croo (Orkney, Scotland, UK; 58°58.9N; 3°23.9W; Fig. 1A) forms part of the European Marine Energy Centre (EMEC)'s network of testing sites for marine renewable energy devices (www.emec.org.uk). The site is exposed to strong north Atlantic swells and provides five cabled test berths in 50–70 m depth, ∼2 km from shore and ∼0.5 km apart, to test full-scale wave energy generators under exposed sea conditions. As part of the Hebridean Marine Energy Futures (HMEF) project, C-PODs were deployed around two adjacent test berths, used for testing Pelamis P2 (P-P2) floating wave attenuators (180 m long; Yemm et al., 2012). Due to P-P2 responsive movement under changing wave conditions, all C-POD moorings had to be placed at least 250 m away from the P-P2 central anchoring assemblage (consisting of a flexible yoke, lengths of chain and embedment anchors). Both berths contained identical mooring and cable infrastructure for P-P2 device attachment (Fig. 1A). There was a variety of other vessel activity across the wave energy site during this study.

An array of seven C-POD moorings was deployed at the wave energy site through the autumn/winter from 26/09/2013 until 02/01/2014 to explore spatial distribution of echolocating porpoises relative to the P-P2 anchor assemblages (Fig. 1A). All C-POD
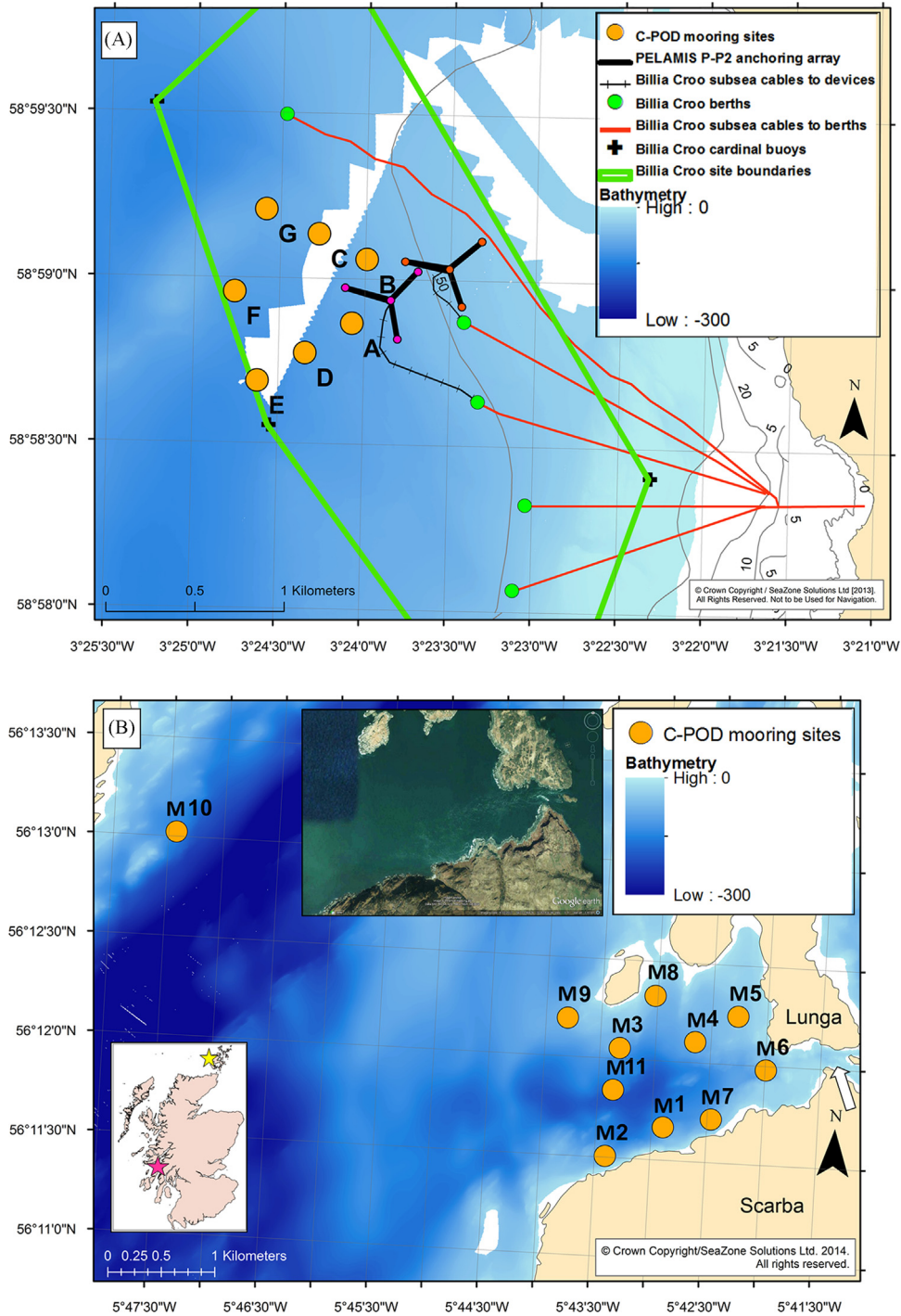
Fig. 1. Overview of C-POD arrays. (A) Billia Croo (yellow star in inset map). EMEC test site boundaries, P-P2 anchoring assemblage and subsea cable infrastructure are also indicated (courtesy of EMEC). (B) Scarba (red star in inset map). Note Grey Dogs tidal channel (white arrow) to the east of Mooring 6, and example of westward tidal flow during flood tide (Google Earth inset). Bathymetry data were derived from the UK Hydro-graphic Office (Billia Croo) and from the INTERREG INISHydro project (Scarba). Gaps in bathymetry are shaded white. Google Earth inset image LandSat; Image © 2016 GetMapping plc; Data SIO, NOAA, US Navy, NGA, GEBCO.

moorings were deployed at depths of 56–69 m, with one C-POD at ~5 m and another at ~15 m above the seabed. Six C-POD moorings were deployed in two linear transects (A–D–E and B–C–G). These transects ran approximately southwest and northwest away from the two P-P2 mooring systems (Fig. 1A) to assess potential impacts on porpoise detections. A seventh C-POD mooring (F) was deployed midway between the E- and G-moorings to collect additional data in this area. Minimum inter-mooring distances ranged from ~300–515 m across an area of approximately 950x800 m. All C-

POD moorings were deployed within the wave energy site boundaries to avoid interactions with fisheries.

2.2. Deployment: Tidal-stream site

The Scarba tidal-stream site (Inner Hebrides, Scotland, UK; 56° 12.0′N; 5° 42.7′W; Fig. 1B) consists of an embayment ~1.5 km across, bounded by several islands but exposed to the west. It is influenced by tidal flows through a narrow channel to the east known locally as the Grey Dogs, where peak flows can reach

speeds of 5 m/s (although this weakens rapidly beyond the narrows). The site was chosen because of consistent presence of harbour porpoises (Benjamins et al., 2016). An array of 10 moorings was deployed across the site in summer from 20/06/2014 until 19/08/2014, allowing for high-resolution assessment of porpoise acoustic distribution. An eleventh mooring was deployed ~5 km away for comparison. Moorings were deployed in 35–114 m of water, with two C-PODs attached to the same mooring within ~5 m above the seabed (apart from mooring 1, which had the C-PODs near the surface for logistical reasons). Minimum inter-mooring distances were ~450–600 m linear distance across an area of approximately 1.6x2 km² (Fig. 1B). As other experiments involving ship movement and acoustic disturbance occurred concurrently at the tidal-stream C-POD array, porpoise detections during this period (n=6 days) were not used for subsequent analyses.

2.3. Analysis

Prior to further analysis, datasets from both C-PODs on each mooring were compared using heteroscedastic t-tests (Zar, 1999) to confirm that they had sampled comparable datasets, which turned out to be the case. Therefore, if both C-PODs on each mooring were still functioning upon recovery, one C-POD was selected at random for processing. If one or both C-PODs had failed before recovery, the unit which had operated the longest was selected. C-POD data were processed using the POD.exe software (v.2.040, Chelonia Ltd., 2015). Only clicks classified as "Moderate" or "High" quality were used in subsequent analyses (Carlström, 2005). A randomly selected subsample of 5% of the raw data with porpoise detections during the final experiment was checked visually to ensure there were no false positives.

All C-POD data were initially analysed at a temporal resolution of whole minutes, with each minute classified as 1 or 0 on the basis of presence/absence of porpoise click trains. Minutes were then designated as Porpoise-Positive Minutes (PPMs) on the basis of click train presence. Wave energy site data were subsequently analysed at the level of Porpoise-Positive Hours (PPH) to better match environmental datasets (see below for details).

Inter-mooring variability in porpoise detection rates was first analysed using summary statistics and contingency table analyses (Zar, 1999). Porpoise presence was subsequently modelled across each array as well as at each individual mooring within both arrays, using a binomial Generalised Additive Modelling (GAM) framework with an independent correlation structure and a logit-link function to determine explanatory relevance of environmental covariates, using the software package R (v.3.0.1; R Core Team, 2013). In these models, the response variable (porpoise presence per unit time) was defined as a binary record (1=presence and 0=absence). Generalised Estimation Equations (GEEs; Liang and Zeger, 1986) were used to address temporal autocorrelation, as described by Pirotta et al. (2011). The independent correlation structure was used because of uncertainty in the actual underlying structure within the datasets, and because GEEs are considered robust against correlation structure misspecification (Liang and Zeger, 1986; Pan, 2001). The logit link function was chosen because it allowed the probability of porpoise detections to be modelled as a linear function of covariates, one of the core assumptions of GEEs (Zuur et al., 2009; Garson, 2013). Temporal autocorrelation was investigated using the R autocorrelation function acf function within the stats package (Venables and Ripley, 2002; threshold=0.05) to define blocks of data within which uniform autocorrelation was expected (using GEEs; Liang and Zeger, 1986; Garson, 2013). Block sizes varied from 49 to 431 min between tidal-stream site moorings, and from 2 to 4 h between wave energy site moorings.

Table 1
Summary of response variables and covariates considered for wave energy site and tidal-stream site modelling efforts.

Parameter	Wave energy site	Whole array	Indiv. moorings	Tidal-stream site	Whole array	Indiv. moorings
Response variable	PPH			PPM		
C-POD ID code	7 individual identifiers, 1 per mooring	F	Not used	11 individual identifiers, 1 per mooring	F	Not used
Diel Hour (GMT)	0–23 h	CY	CY	0–23 h	CY	CY
# of days since deployment (Date)	1–51	F	F; L	1–61 (excluding days 18–21, 32–33 to avoid influence of other experiments; 55 actual full days)	F	F; CB
Avg. C-POD angle (°)	Downward deflection from vertical, where 0° = C-POD pointing straight up, averaged per hour (0–50°)	CB	L; CB	Downward deflection from vertical, where 0°=C-POD pointing straight up (0–124°)	L	L; CB
Substrate composition	Sandy gravel (5x), gravelly sand (2x)	F	Not used	Rock (3x), Sand (3x), Muddy sand (4x), Sandy mud (1x)	F	Not used
Avg. Significant Wave Height H_{m0}	Four times the standard deviation of the surface elevation (cm) received by WaveRider buoy, averaged per hour	CB	CB	N/A		
Avg. Sea Surface Temperature (°C)	Sea surface temperature (°C) recorded by WaveRider buoy, averaged per hour	CB	CB	N/A		
% of minute lost	Fraction of each minute lost due to ambient noise, averaged per hour	CB	L; CB	Fraction of each minute lost due to ambient noise, measured per minute	CB	L; CB
Water depth (m)	Water depth (m) at mooring site relative to Chart Datum	CB	Not used	Water depth (m) at mooring site relative to Chart Datum	CB	CB
Distance to P-P2 anchoring assemblage (m)	Linear distance between closest P-P2 anchoring assemblage and C-POD moorings A–G	CB	Not used	N/A		
Closest distance to shore (m)	Linear distance between mooring and nearest shore	CB	Not used	Linear distance between mooring and nearest shore	CB	Not used
Tidal phase	0=1=Low Tide at Stromness	CY	CY	0=1=Low Tide at Oban	CY	CY

Note that response variables varied between arrays. Initial covariate treatments in each model are abbreviated as follows: F=Factor; L=Linear term; CB=cubic B-spline; CY=cyclic spline.

General modelling approaches followed those outlined in more detail by Pirotta et al. (2011). Data exploration protocols were used to identify outliers, data variability, relationships between covariates and response variable, and collinearity between covariates (Zuur et al., 2010; Zuur, 2012). Modelling was initiated using a basic GLM to assess collinearity of covariates, following Zuur (2012). Collinear covariates were identified using the *vif* (Variance Inflation Factor) function within the R package *car* (v.2.0-20; Fox and Weisberg, 2015) and using a stepwise procedure the covariates with the highest VIF value (exceeding 3) were removed.

Response variables and covariates used for modelling varied between the two sites (Table 1). Environmental covariates were selected for each site on the basis of their availability at appropriate spatiotemporal scales, as well as potential relevance to porpoise presence and/or detectability. Various studies have indicated a preference by harbour porpoises for nearshore habitat in moderate (> 50 m) water depths (e.g., Embling et al., 2010; Isojunno et al., 2012; Booth et al., 2013), informing the use of Depth (m) and Closest Distance to Shore (m). The potential effect of the tidal cycle on porpoise detections was investigated based on harmonic analysis (POLTIPS-3™ tidal prediction software). The duration of each tidal cycle was derived from tidal predictions for the nearby ports of Oban ($\sim$33 km from the tidal-stream site) and Stromness ($\sim$7 km from the wave energy site). Each minute or hour within each cycle was then assigned a numeric value between 0 and 1 relative to Low Tide ($0 = 1 =$ Low Tide at Oban/ Stromness). Tides here were generally semidiurnal (average duration 12.4 h), although individual cycle durations varied according to the spring-neap cycle. The Tidal Phase parameter, as used here, represents a proxy for expected tidal strength and direction which were not measured at either site. C-POD angle was included as a statistical control because C-PODs' omnidirectional sensitivity can be affected if devices are pulled sideways by currents. Similarly, % of each minute lost was included as it results in reduced monitoring effort, thereby potentially reducing the probability of porpoise detection.

In addition to the above covariates, the wave energy site models also included data on Average Significant Wave Height (cm) and Average Sea Surface Temperature (°C), derived from the EMEC WaveRider™ wavebuoy stationed at the wave energy site. Little is known about how porpoise behaviour or their detectability is influenced by wave conditions; during periods of large waves (e.g., storms), animals might change their distribution, become more difficult to detect due to increasing ambient noise levels, or might change vocalisation rates. In the present models, wave activity was considered as a potential influence on porpoise detectability. Temperature was included as another measure of larger-scale environmental variability that might influence porpoise prey. As these data were only available at a 30-min resolution, the wave energy site C-POD data were modelled at a temporal scale of hours, to allow wavebuoy data to be incorporated into the models at appropriate resolution. As mentioned earlier, a new binary response variable 'Porpoise-Positive Hour' (PPH) was therefore defined, where $1 = \geq 1$ PPM detected per hour and $0 =$ no PPMs detected. All the covariates were considered as linear terms, as factors, as 1-dimensional smooth terms (4 degrees of freedom) modelled as cubic B-splines with one internal knot positioned at the average value of each variable, or as cyclic splines based on variance-covariance matrices.

Model selection was based on using the Quasi-likelihood under Independence model Criterion (QIC_u, a modification of Akaike's Information Criterion appropriate for GEE models, available through the R library *yags* v.4.0-2.2; Akaike, 1974; Pan, 2001; Carey, 2004). Covariates were removed from the model using backwards stepwise model selection, until no further covariates could be removed without causing the QIC_u score to increase, following Pirotta et al. (2011). How each covariate should be treated within each model (as a factor, a linear term, or a spline) was determined in a similar fashion. Final models were fitted using the R function *geeglm* from the R library *geepack* v.1.1-6 (Halekoh et al., 2006) to assess the statistical significance of remaining covariates. The Wald's Test (Hardin and Hilbe, 2003) was used to determine each covariate's significance using the R package *stats*. Non-significant covariates were removed from the model using backwards stepwise model selection and the obtained model re-tested until all associated p-values of remaining covariates were < 0.05, resulting in the final model. Final model performance was evaluated through presence–absence confusion matrices summarising the models' goodness of fit (Fielding and Bell, 1997). Such matrices require selection of a cut-off point beyond which a prediction is considered a presence (Pirotta et al., 2011). Confusion matrices were generated using Receiver Operating Characteristic (ROC) curves, which plot the
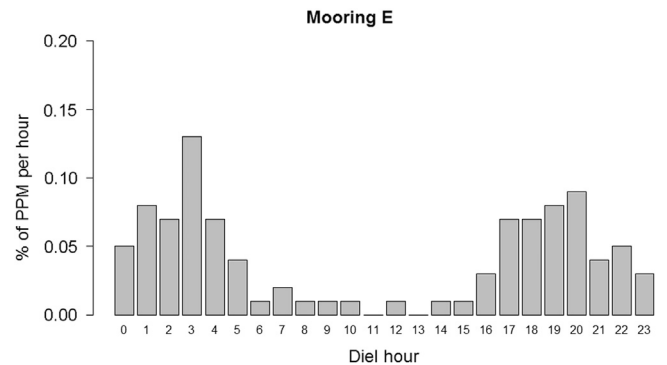
Fig. 2. Example of diel pattern in Porpoise-Positive Minutes (PPM) at mooring E at the wave energy site (data aggregated by hour (GMT) across entire deployment period).

Table 2

Summary of C-POD array data from selected C-PODs. (A) Wave energy site. All data presented here cover a 51-day period from 05/10-24/11/2013 when all C-PODs were active. (B) Tidal-stream site. All data presented here cover a 55-day period from 21/06-17/08/2014 when all C-PODs were active (not including six days due to potential interference by other experiments; mooring M11 was only deployed for 34 days; see text for details).

(A)

Wave energy site	A	B	C	D	E	F	G				
# of PPMs detected	354	220	462	523	753	707	413				
Average daily PPM detection rates	6.9	4.3	9.1	10.3	14.8	13.9	8.1				

(B)

Tidal-stream site	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11
# of PPMs detected	1629	909	1658	1760	1195	527	1479	2535	2323	1861	1490
Average daily PPM detection rate	31.9	17.8	32.5	34.5	23.4	10.3	29.0	49.7	45.5	36.5	29.2

proportion of correctly classified presences against the proportion of incorrectly classified presences, using the R library *ROCR* v.1.0-5 (Sing et al., 2009). The most appropriate cut-off points were determined by calculating the point where the maximum distance between the ROC curve and a 45° diagonal was observed. In addition, Area Under Curve (AUC) calculations were used to evaluate overall model performance (range: 0.5–1; the closer AUC approaches 1, the better the model; Boyce et al., 2002), again using the R library *ROCR* v.1.0-5.

Probabilistic model outputs were generated for each covariate in the final models, plotted against the response scale as per Pirotta et al. (2014). Confidence intervals around these plots were computed following Genz and Bretz (2009) with the *mvtnorm* package v.0.9-99992 (Genz et al., 2015). An example of an R script employing the above modelling approach is included as Supplementary material.

3. Results

3.1. Wave energy site: initial analysis

All C-PODs regularly detected porpoise click trains during the deployments (Table 2), although detection rates varied from day to day. There was no significant difference in PPM detection rates per day between the paired C-PODs at single moorings. One C-POD failed before deployment, vindicating the use of two C-PODs per mooring. Most C-PODs' batteries had been depleted when the array was recovered in January 2014. Although some C-PODs functioned for up to 98 days, the entire array (i.e., at least one C-POD at all 7 moorings) functioned for 58 full days until 25 November 2013. In the event, the P-P2 device was only present from 26/09/2013 until 4/10/2013, reducing its relevance as a covariate; as a result, the present analysis only covers the 51-day period after the removal of the P-P2 device (while retaining the mooring assemblage), from 5/10/2013 until 24/11/2013.

Across the wave energy site array, average daily PPM detection rates varied, but most noticeably between moorings at opposite ends of the array (Table 2). Specifically, average daily detection rates at western moorings E and F were more than double those at moorings A and B, near the P-P2 mooring assemblage. All moorings recorded significant diel variability in detection rates, with a notable peak in detections between ~17:00 and 07:00, which was consistent across all moorings ($\chi^2 = 1.4462$, d$f = 138$, $p = 0.99$; Fig. 2).

3.2. Wave energy site: modelling results

As described above, models of wave energy site moorings used data at temporal scales of hours, rather than minutes. The final model structures (most important covariates first, with
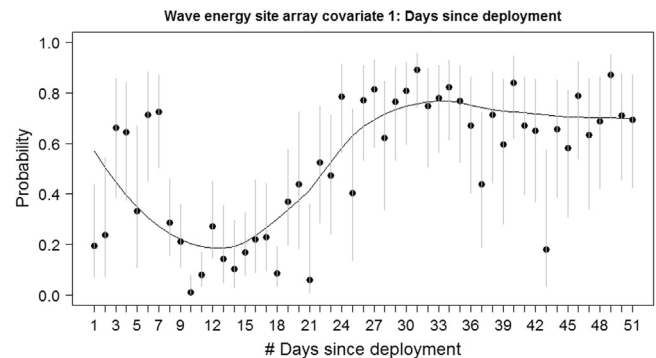

Fig. 3. Daily variability in PPM detection probability across the wave energy site array (data from all moorings combined) from Days 1 through 51 (5/10/2013–24/11/2013). A fitted line was generated using a 2nd-order LOESS smoothing curve (span=0.7).

Table 3
Summary of model performance (AUC, confusion matrices [transformed into %]) and Wald's test results for all significant covariates for the final models for all 11 individual wave energy site moorings and the entire array. Most important covariates for each model are at the top, with subsequent covariates below. Percentages indicate for each model what fraction of predicted porpoise detection events (Porp. vs. No Porp.) corresponded to actual observations at each site. Bold, underlined values = correctly predicted fractions, *italic values* = incorrectly predicted fractions. High bold, underlined values indicate a better working model.

Model	AUC	Confusion matrix	Observed		Wald's Test				
			Porp.	No Porp.	Parameter	ΔQICu	DF	χ^2 score	P
Whole array	0.78	**Predict.**			Date	339.72	50	295.1	< 0.001
		Porp.	**71%**	*29%*	Diel Hour	234.81	4	148.5	< 0.001
		No porp.	*29%*	**71%**	Avg. Sig. Wave Ht.	57.73	4	63.9	< 0.001
					Location	21.63	6	64.1	< 0.001
					Tidal phase	19.80	4	29.9	< 0.001
					% Time Lost	19.58	4	16.8	0.002
					Avg. C-POD Angle	4.28	4	12.0	0.017
A	0.59	Porp.	**68%**	*39%*	% Time Lost	5.73	1	4.2	0.041
		No porp.	*32%*	**61%**	Date	2.77	1	4.2	0.041
B	0.71	Porp.	**75%**	*41%*	Diel Hour	14.72	4	15.8	0.003
		No porp.	*25%*	**59%**	% Time Lost	14.19	4	29.9	< 0.001
C	0.66	Porp.	**55%**	*32%*	Diel Hour	16.77	4	16.4	0.003
		No porp.	*45%*	**68%**	% Time Lost	10.38	4	11.3	0.024
D	0.74	Porp.	**65%**	*27%*	Diel Hour	33.43	4	18.0	0.001
		No porp.	*35%*	**73%**	Date	2.17	4	13.1	0.011
					Avg. C-POD Angle	1.25	4	13.6	0.009
E	0.71	Porp.	**76%**	*44%*	Diel Hour	41.73	4	27.3	< 0.001
		No porp.	*24%*	**56%**	Date	13.71	1	11.8	< 0.001
					Tidal phase	3.47	4	12.1	0.016
F	0.70	Porp.	**72%**	*38%*	Diel Hour	56.07	4	35.7	< 0.001
		No porp.	*28%*	**62%**	Date	5.47	1	5.3	0.022
G	0.68	Porp.	**87%**	*60%*	Diel Hour	0.52	4	30.0	< 0.001
		No porp.	*13%*	**40%**					

subsequent covariates explaining smaller and smaller amounts of variation) are described below (Table 3).

The final wave energy site models reiterated the importance of the observed diel pattern in detections, with Diel Hour the most significant covariate for almost all moorings (Table 3). Diel Hour displayed a notable bimodal distribution suggesting increased detection probability around dawn and dusk. Date was important for several moorings across the array, suggesting short-term daily variability in detection probability (Fig. 3). Average Significant Wave Height was of limited importance for the whole array model, but was not retained in any of the individual mooring models. Tidal phase was only retained as a covariate for mooring E. The relevance of Average C-POD angle for porpoise detections at Mooring D was unclear.

3.3. Tidal-stream site: initial analysis

As at the wave energy site, all C-PODs regularly detected porpoise click trains during the deployment (Table 2). All C-PODs but one remained active during the entire deployment period (61

days, of which only 55 were analysed). Mooring M11 was deployed six days after the others to fill a potential gap in the array. One week after its deployment, this same mooring was accidentally removed by a local fisherman and was only replaced after ~20 days, after which it continued to function until recovery of the array. One of the M1 C-PODs failed soon after deployment for unknown reasons, although the other in its pair continued to function.

Considerable heterogeneity in porpoise detections was apparent across the tidal-stream site array. Daily porpoise detection rates at the various tidal-stream moorings were quite different, with more detections observed at moorings in more exposed, open waters. Moorings fell into two distinct categories: one containing moorings set in the core of the embayment, as well as M10, with relatively high daily detection rates and another containing more peripheral moorings (particularly M2, M6 and M8) with lower daily detection rates (Table 2). Moreover, diel detection patterns (with all data aggregated by hour) also varied significantly across the array ($\chi^2 = 6438.182$, d$f = 230$, $p < 0.001$; Fig. 4). In the northern part of the array (M5, M6 and M8 in particular) a notable diel pattern was observed, with almost all
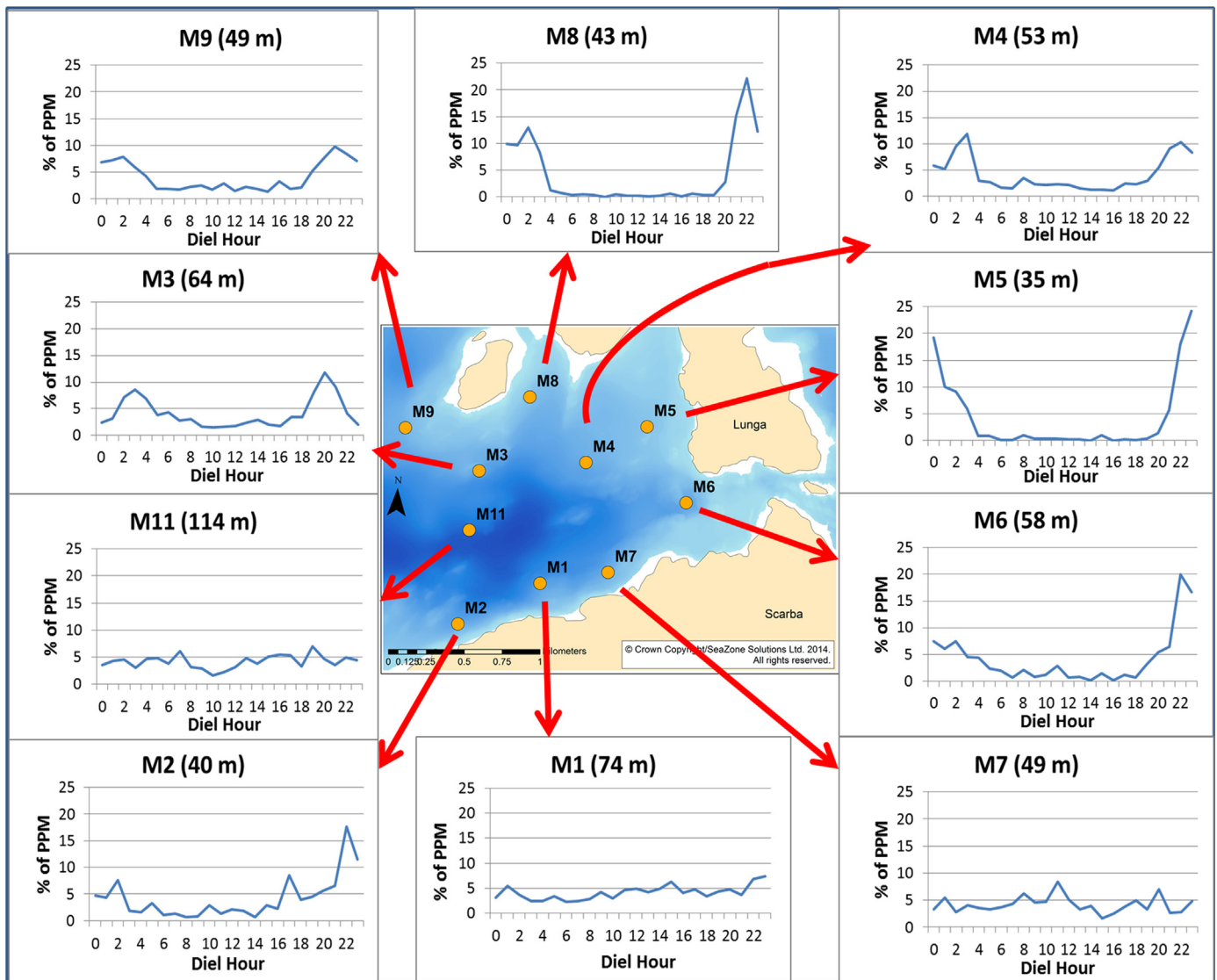

Fig. 4. Distribution of % of total PPM detections by diel hour (0–23 h) across the tidal-stream array, aggregated over entire deployment period. Results from peripheral mooring M10 are not shown. Mooring deployment depths (m) are indicated.

Table 4

Summary of model performance (AUC, confusion matrices [transformed into %]) and Wald's test results for all significant covariates for the final models for all 11 individual tidal-stream site moorings and the entire array. Most important covariates for each model are at the top, with subsequent covariates below. Percentages indicate for each model what fraction of predicted porpoise detection events (Porp. vs. No Porp.) corresponded to actual observations at each site. <u>Bold, underlined values</u> = correctly predicted fractions, *italic values* = incorrectly predicted fractions. High <u>bold, underlined</u> values indicate a better working model.

Model	AUC	Observed		Wald's Test				
		Porp.	No Porp.	Parameter	ΔQIC_u	DF	χ^2 score	P
Whole array	0.73	**Pred.**		Date	5334.92	54	369.9	< 0.001
		<u>**70%**</u>	*36%*	Diel Hour	5169.90	4	314.6	< 0.001
		30%	<u>**64%**</u>	Depth (m)	1002.56	4	157.6	< 0.001
				Tidal Phase	281.40	4	32.7	< 0.001
				C-POD angle	266.09	1	22.4	< 0.001
				% Time lost	135.72	4	45.5	< 0.001
M1	0.76	<u>**72%**</u>	*31%*	Date	877.37	54	334.1	< 0.001
		28%	<u>**69%**</u>	Tidal phase	179.93	4	18.9	< 0.001
M2	0.81	<u>**77%**</u>	*39%*	Diel Hour	384.14	4	43.5	< 0.001
		23%	<u>**61%**</u>	C-POD Angle	136.77	4	63.1	< 0.001
				% Time lost	32.69	4	68.0	< 0.001
				Tidal phase	12.54	4	17.2	0.002
M3	0.77	<u>**74%**</u>	*32%*	Date	771.20	54	264.0	< 0.001
		26%	<u>**68%**</u>	Diel Hour	44.16	4	36.6	< 0.001
				Tidal phase	24.02	4	11.4	0.023
				% Time lost	8.51	1	6.5	0.011
M4	0.78	<u>**69%**</u>	*26%*	Date	1474.31	54	310.0	< 0.001
		31%	<u>**74%**</u>	Diel Hour	948.19	4	67.3	< 0.001
				Tidal phase	114.02	4	24.2	< 0.001
M5	0.88	<u>**86%**</u>	*21%*	Diel Hour	2746.70	4	240.9	< 0.001
		14%	<u>**79%**</u>	Date	253.44	4	19.4	< 0.001
M6	0.81	<u>**79%**</u>	*29%*	Diel Hour	454.65	4	86.4	< 0.001
		21%	<u>**71%**</u>	% Time lost	128.20	4	33.2	< 0.001
				Date	72.27	1	20.5	< 0.001
				Tidal phase	58.18	4	35.8	< 0.001
M7	0.80	<u>**76%**</u>	*31%*	Date	1257.12	4	92.5	< 0.001
		24%	<u>**67%**</u>	Tidal phase	870.94	4	99.8	< 0.001
				Diel Hour	3.40	4	10.1	0.039
M8	0.83	<u>**93%**</u>	*31%*	Diel Hour	4321.35	4	387.8	< 0.001
		7%	<u>**69%**</u>					
M9	0.71	<u>**71%**</u>	*40%*	Diel Hour	829.84	4	84.8	< 0.001
		29%	<u>**60%**</u>	Date	418.87	4	53.1	< 0.001
				C-POD angle	74.85	1	18.6	< 0.001
				Tidal phase	5.14	4	13.0	0.011
M10	0.64	<u>**70%**</u>	*48%*	Date	154.24	54	168.3	< 0.001
		30%	<u>**52%**</u>	Diel Hour	20.32	4	10.9	0.028
M11	0.68	<u>**58%**</u>	*31%*	Date	205.66	35	121.7	< 0.001
		42%	<u>**69%**</u>	Diel Hour	10.51	4	21.8	< 0.001
				Tidal phase	125.41	4	39.8	< 0.001

detections occurring at night. This pattern was largely absent from more southern moorings (M1, M7 and M11) as well as from M10.

3.4. Tidal-stream array: modelling results

All covariates remained statistically significant for the model of the entire array, but different combinations of covariates were selected for different moorings (Table 4).

Date was an important predictor variable for all moorings, reflecting a general decline in porpoise detection rates towards the end of the deployment period. Detection probability at moorings adjacent to the Grey Dogs tidal flow (particularly M1, M6, M7 and M11) was also influenced by tidal phase. Elsewhere, most notably at M5 and M8, Diel Hour had a significant effect on detection probability. The selected model suggested that porpoise detection probability varied considerably across the embayment in response to localised conditions. For example, while detections at both M3 and M7 were influenced by tidal phase, the probability of detecting porpoises was highest earlier in the tidal cycle at M7 (peak at ~0.2) than at M3 (peak at ~0.4) due to M7's location

(Fig. 5). Westward flow (on flooding tides) was important at southern moorings (M1, M 7, and M 11) whereas periods around or immediately after slack tide (~0 and ~0.5) were more important at M3 and M9. Eastward flow on ebbing tides appeared only important at central moorings (M4 and M6; Fig. 5). Some covariates (e.g., % Time Lost) were significant for specific moorings but did not reveal a clear pattern.

4. Discussion

The results from the two case studies described above have highlighted the extent to which porpoise detection rates differed across the arrays. While it is not necessarily surprising that a heterogeneous tidal habitat is not used uniformly by a mobile species such as harbour porpoise, these results indicated significant spatiotemporal heterogeneity in porpoise habitat use amongst closely spaced moorings hundreds of metres apart. Even at the otherwise relatively homogeneous wave energy site (in terms of bathymetry), spatiotemporal variability was indicated.
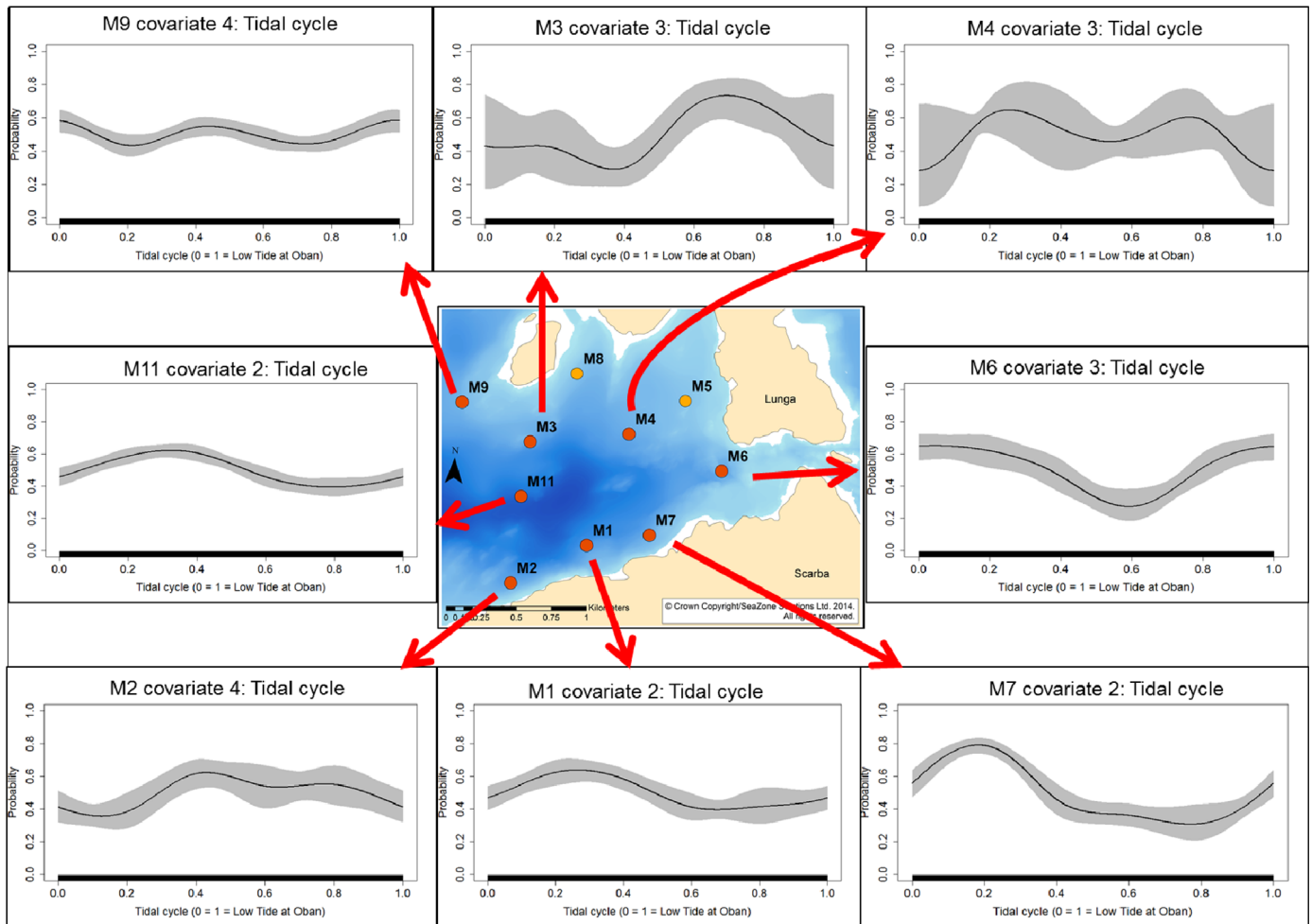
Fig. 5. Effect of tidal phase (0=1=Low Tide at Oban) on predicted PPM detection probability (± 95% CI's) across the tidal-stream site array (after Pirotta et al., 2011) for those moorings where tidal cycle was a significant covariate in final models (Table 4). Vertical axes depict the probability of porpoise detections across the tidal cycle. Results from peripheral mooring M10 are not shown.

The results presented here should be considered as examples of variability in habitat use of echolocating harbour porpoises in energetic marine environments, rather than a direct comparison between the two sites, which were studied under different projects in different seasons.

For the wave energy site array, the main difference between moorings was the low daily PPM detection rates at moorings A and B, furthest inshore but also adjacent to the P-P2 anchoring assemblage, relative to the other moorings (Table 2). Although the presence of the P-P2 device was not used as a covariate in the wave energy site models (as it was mostly absent during the array deployment), and data collected during deployment were excluded, it is conceivable that noise produced by the anchoring assemblages could have deterred porpoises. Alternatively, the observed patterns may result from fine-scale habitat preferences (e.g., slightly deeper waters, distribution of prey; Johnston et al., 2005; Marubini et al., 2009; Embling et al., 2010). It is unknown how porpoises were distributed across the area before the P-P2 mooring assemblages were deployed, complicating the choice between these alternatives. Benthic habitat surveys across the wave energy site suggest predominantly mixed sediments (sands and gravels; Aurora Environmental Ltd., 2009; Jackson, 2014) without distinct bathymetric features. Fine-scale distribution data of porpoise prey species (particularly sandeels *Ammodytidae* and gadoid fish; Santos et al., 2004) are lacking. Jackson (2014) measured tidal currents around the P-P2 mooring assemblages across different tidal phases using a Teledyne 300 kHz Acoustic Doppler Current Profiler (ADCP).

Current speeds generally did not exceed 0.7 m s^{-1} but varied considerably in strength and directionality between flood and ebb, as well as at relatively small spatial scales (hundreds of metres) and vertically across the water column. This suggests a more complex spatio-temporal current pattern than might otherwise be suspected based solely on bathymetry. The significance of this variability to porpoises and their prey is presently unknown.

For the tidal-stream site array, significant differences were found in detection rates across the array in response to various factors, most notably diel hour and tidal phase. Certain inshore areas relatively unaffected by tides (e.g., moorings 5 and 8; Fig. 3), appear to have been mainly visited at night. In contrast, detection rates at other moorings (e.g., moorings 1, 6, 7 and 11) were much more heavily influenced by the tidal stream of the Grey Dogs. This suggests that porpoise distribution in these sorts of environments can be highly heterogeneous at small spatiotemporal scales. Adjacent PAM sensors should not be assumed to provide similar results; conversely, comparable porpoise detection patterns at more distant PAM sensors (e.g., moorings 2 and 5) suggested similar site use across non-adjacent sections of the array. Although much still remains to be discovered about porpoise habitat use in tidal sites, evidence to date suggests considerable spatiotemporal variability in distribution related to ephemeral tidal features such as jets, eddies and overfalls (Pierpoint, 2008; Wilson et al., 2013; Wood et al., 2014). Tidal strength and direction are known to vary predictably in such sites, and the observed patterns of detection probability across the tidal-stream site array suggest that porpoises utilise particular locations

(such as the area influenced by the jet from the Grey Dogs) only under specific tidal conditions. Numerous observations of porpoises and other cetaceans in tidal-stream sites worldwide suggest that such conditions result in improved foraging opportunities for porpoises (reviewed in Benjamins et al., 2015). At present it remains unclear whether increased prey abundance or heightened prey vulnerability to predation in fast flow is a more important driver of porpoise presence in tidal-stream environments.

Because results were somewhat similar between adjacent moorings, the present array configurations provided a workable compromise between studying high-resolution porpoise habitat use and practicalities of array deployment and recovery in energetic waters, with C-PODs spaced ∼300–600 m apart. If these inter-mooring distances were applied across larger sites, average mooring densities would range between approximately 4 and 16 moorings km^{-2}. Costs of maintaining such arrays may be considerable, although these would be offset to some extent by reduced risk of PAM device failure or mooring loss, and may still be comparable to other survey methods (Thompson et al., 2014). It is unclear whether a denser array design with substantially more C-PODs would describe even greater heterogeneity. If the array were extremely dense, C-POD detection ranges would begin to significantly overlap, and individual porpoises might be detected by multiple C-PODs (acknowledging directionality and narrowness of porpoises' echolocation beams; Koblitz et al., 2012). Many adjacent stations would then provide redundant information, effectively wasting effort and resources. On the other hand, if the array were too sparse, variability at spatial scales much smaller than the minimum inter-mooring distance might be underestimated.

The results from both arrays imply that porpoises can display large and consistent spatiotemporal variability in site use at scales as small as hundreds of metres and within hours. This variability is most probably driven by environmental heterogeneity, which is likely to be particularly important in and around nearshore tidal-stream sites. Small-scale variability in presence and extent of tidally-driven oceanographic features is a likely important driver for porpoise distribution within such sites (Benjamins et al., 2015). This has implications for monitoring efforts to assess potential impacts of coastal developments on porpoises, including MRED construction and operation. Although official MRED monitoring guidance may recommend use of multiple PAM moorings (e.g., Macleod et al., 2011), use of PAM as a cetacean monitoring tool is not standardised and approaches vary between developers (HWDT, 2010; MeyGen, 2012; Wilson et al., 2012). Inter-mooring differences in click detectors among moorings across the wave energy site array were modest except when comparing extreme ends of the array, but the tidal-stream site array displayed significant variability across multiple moorings. While deploying a single PAM mooring in this kind of environment will illustrate local temporal variability in porpoise presence, it will likely provide an unrepresentative picture of harbour porpoise habitat use across the area. Moreover, placement decisions of a solitary PAM mooring within a heterogeneous development site could have profound consequences for interpretation of the final results in terms of risks faced by porpoises if porpoise distribution is incorrectly assumed to be uniform. PAM arrays therefore appear to be a more appropriate tool to study site-specific cetacean habitat use and assess potential impacts of coastal developments at small spatiotemporal scales, particularly in heterogeneous environments such as tidal streams. Practical constraints (e.g., limited resources) may limit the scope of such monitoring schemes. However, irrespective of which method is used, monitoring efforts should be designed to collect data at appropriate spatiotemporal scales to generate relevant data for management. This is particularly important as more complex monitoring programmes are being implemented (as is presently the case in EU waters through the EU Marine Strategy Framework Directive (MSFD), to ensure the marine environment achieves Good Environmental Status by 2020). If monitoring efforts under MSFD and other programmes are to be used to detect long-term trends, then this work emphasises the need to understand and account for minor (seemingly trivial) differences in siting location between successive sensor deployments for monitoring these mobile and otherwise wide ranging species.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr2.2016.07.002.

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