


Spatiotemporal variation in harbor porpoise distribution and foraging across a landscape of fear

Laura D. Williamson^{1,2,3}  | Beth E. Scott²  | Megan R. Laxton⁴  |
Fabian E. Bachl⁵ | Janine B. Illian⁴  | Kate L. Brookes⁶  |
Paul M. Thompson⁷ 

¹Ocean Science Consulting Limited, Dunbar, UK

²School of Biological Sciences, University of Aberdeen, Aberdeen, UK

³Environmental Research Institute, University of the Highlands and Islands, Thurso, UK

⁴School of Mathematics and Statistics, University of Glasgow, Glasgow, UK

⁵School of Mathematics, University of Edinburgh, Edinburgh, UK

⁶Marine Scotland Science, Marine Laboratory, Aberdeen, UK

⁷Lighthouse Field Station, School of Biological Sciences, University of Aberdeen, Cromarty, UK

Correspondence

Laura D. Williamson, Ocean Science Consulting Limited, Spott Road, Dunbar EH42 1RR, UK.
Email: lw@osc.co.uk

Funding information

Marine Alliance for Science and Technology for Scotland; Marine Scotland Science; University of Aberdeen

Abstract

Understanding spatiotemporally varying animal distributions can inform ecological understanding of species' behavior (e.g., foraging and predator/prey interactions) and support development of management and conservation measures. Data from an array of echolocation-click detectors (C-PODs) were analyzed using Bayesian spatiotemporal modeling to investigate spatial and temporal variation in occurrence and foraging activity of harbor porpoises (*Phocoena phocoena*) and how this variation was influenced by daylight and presence of bottlenose dolphins (*Tursiops truncatus*). The probability of occurrence of porpoises was highest on an offshore sandbank, where the proportion of detections with foraging clicks was relatively low. The porpoises' overall distribution shifted throughout the summer and autumn, likely influenced by seasonal prey availability. Probability of porpoise occurrence was lowest in areas close to the coast, where dolphin detections were highest and declined prior to dolphin detection, leading potentially to avoidance of spatiotemporal overlap between porpoises and dolphins. Increased understanding of porpoises' seasonal distribution, key foraging areas, and their relationship with competitors

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 The Authors. *Marine Mammal Science* published by Wiley Periodicals LLC on behalf of Society for Marine Mammalogy.

can shed light on management options and potential interactions with offshore industries.

KEYWORDS

bottlenose dolphin, competition, C-POD, distribution, foraging, harbor porpoise, INLA, landscape of fear

1 | INTRODUCTION

Heterogeneous environments result in patchy distribution of resources (Fauchald, 2009), resulting in an irregular distribution of animals to maximize their foraging efficiency (Benoit-Bird et al., 2013). Unraveling the drivers (and appropriate proxies to use during modeling) of these spatially and temporally varying distributions is important to inform our ecological understanding of the species, as well as to support development of effective management and conservation measures (Dunn et al., 2011; Pompa et al., 2011).

The harbor porpoise (*Phocoena phocoena*) is the most abundant cetacean in the North Sea, Northeast Atlantic (Hammond et al., 2017). They are often bycaught in fisheries (Hammond et al., 2002) and encountered in offshore development sites (e.g., Bailey et al., 2010; Brandt et al., 2011; Dähne et al., 2013; Graham et al., 2019; Pirotta et al., 2014). Knowledge of spatiotemporal patterns in both distribution and important foraging locations is therefore required to support management measures to mitigate potential impacts from offshore industries.

Harbor porpoise distribution has been assessed previously in relation to a variety of static (e.g., depth and slope) and dynamic habitat variables. Dynamic variables include sea surface temperature (MacLeod et al., 2007), time of day (Carlström, 2005; Todd et al., 2009; Williamson et al., 2017), chlorophyll-*a* (Philpott, 2013; Wingfield et al., 2017), high tidal flow (Isojunno et al., 2012; Marubini et al., 2009), low tidal flow (De Boer et al., 2014; Embling et al., 2010), flood tide (Johnston et al., 2005), upwelling (Jones et al., 2014; Skov & Thomsen, 2008), tidal stratification, and mixing (De Boer et al., 2014; Hall, 2011; Philpott, 2013); however, relationships between porpoise distribution and these variables are often inconsistent between studies. Associations between animal distribution or behavior and environmental variables (proxies for resource distribution) can change, and interactions with environmental characteristics may vary from region to region (De Boer et al., 2014) or between individuals (Johnston et al., 2005). In addition, differences may be shaped by spatial variation in the presence of competitors or predators that constrain habitat choice in a landscape of fear (Wirsing et al., 2008). Globally, killer whales (*Orcinus orca*) and white sharks (*Carcharodon carcharias*) are the two main predators of porpoises (Read, 1999); however, in some regions they are also killed/harassed by bottlenose dolphins, *Tursiops truncatus* (Jepson & Baker, 1998; Patterson et al., 1998; Ross & Wilson, 1996) and gray seals, *Halichoerus grypus* (Leopold et al., 2015). Porpoises are not targeted as prey by bottlenose dolphins, as there is no evidence that they are ever consumed (Ross & Wilson, 1996); this behavior may instead represent a violent form of interference competition in which top predators kill mesopredators to reduce competition for prey (Ritchie & Johnson, 2009).

Previous studies in areas where these interactions occur have shown that porpoises and dolphins are often detected in the same locations, but there are fine-scale differences in temporal patterns of area use (Nuuttila et al., 2017; Thompson & White, 2004). In Cardigan Bay, Wales (UK), dolphins and porpoises are sympatric, but each has different relationships between occurrence and seasons, time of day, and tidal phase (Nuuttila et al., 2017). In the Moray Firth (MF), harbor porpoises are distributed throughout the entire region with highest occurrence on the sandy Smith Bank, in the outer MF (Brookes et al., 2013; Williamson et al., 2016). In contrast, bottlenose dolphins are primarily found in coastal areas, while detections offshore are usually of other species of dolphin that have not been reported to attack porpoises including common (*Delphinus delphis*), white beaked (*Lagenorhynchus albirostris*), and Risso's (*Grampus griseus*) dolphins (Palmer et al., 2017; Thompson et al., 2014). Other predators such as killer

whales occur only rarely (Waggitt et al., 2020) and, while gray seals are widespread in the MF, there is no evidence of them killing porpoises in this area.

In this study, we used data from a large-scale array of passive echolocation-click detectors (C-PODs) to investigate spatial and temporal variation in occurrence and foraging activity of porpoises, and how this may be influenced by both daylight and the presence of bottlenose dolphins. We used hierarchical Bayesian modeling (HBM) with integrated nested Laplace approximation (INLA) for model fitting (Rue et al., 2009) using the stochastic partial differential equation (SPDE) approach (Lindgren et al., 2011).

2 | METHODS

2.1 | C-POD data

Echolocation-click data were collected in the MF between July and October 2009, 2010, and 2011 (Figure 1). Data were collected using C-PODs (Chelonia Ltd., 2014a) as described by (Brookes et al., 2013; Williamson et al., 2016, 2017). C-PODs were deployed 2–5 m above the seabed at sites ranging in depth from 7–73 m (Figure 1), and data were available from 33–58 sites in each month (Table 1). Data on the occurrence of porpoise and dolphin clicks were extracted using version 2.025 of the cpod.exe software (Chelonia Ltd., 2014b).

2.2 | Response variables

Two different models were fitted to the data: one investigating the spatiotemporal distribution of harbor porpoises and the other investigating porpoise foraging activity (Table 2). Porpoise occurrence data were used to create a binomial response variable representing the presence or absence of harbor porpoises within an hour (DPH), which was then used in the occurrence model (Table 2). This hourly metric was selected to minimize the extent to which the detection probability of a C-POD may be influenced by changes in sensitivity with ambient noise levels (Dähne et al., 2013), tidal flow (Wilson et al., 2013), or deployment depth (Alonso & Nuuttila, 2014).

Buzzes, assumed to be from foraging (Verfuß et al., 2009), were also extracted from acoustic detections based on the duration of interclick interval (ICI) using Gaussian mixture models to assign clicks with different ICIs to different categories (Pirota et al., 2014; Williamson et al., 2017). Echolocation clicks with ICIs of less than 10 ms were from foraging buzzes (Carlström, 2005). A binomial response variable representing presence or absence of porpoise echolocation clicks that were classified as foraging buzzes in each hour (for hours in which detections were made) was created for use in the foraging model (Table 2).

2.3 | Explanatory variables

The number of hours between a porpoise detection and the nearest dolphin detection was calculated for a rolling 24 hr period at each site. This resulted in positive values when the porpoise was detected after the dolphin, and negative when the porpoise was detected before the dolphin. All detections more than ± 24 hr away were excluded. Truncation at 24 hr removed long gaps between detections (when there were no animals present) but retained any potential diel relationships between porpoise and dolphin occurrence.

Sunrise and sunset times were obtained from the POLTIPS oceanographic model (NERC National Oceanography Centre, Liverpool, UK) for the port of Helmsdale, in the MF. These were converted into a continuous cyclic variable, “daylight,” at an hourly resolution in which 0.25 represented sunrise, and 0.75 represented sunset. This daylight variable was used because time of day is not an appropriate metric for investigating light-mediated changes to detection

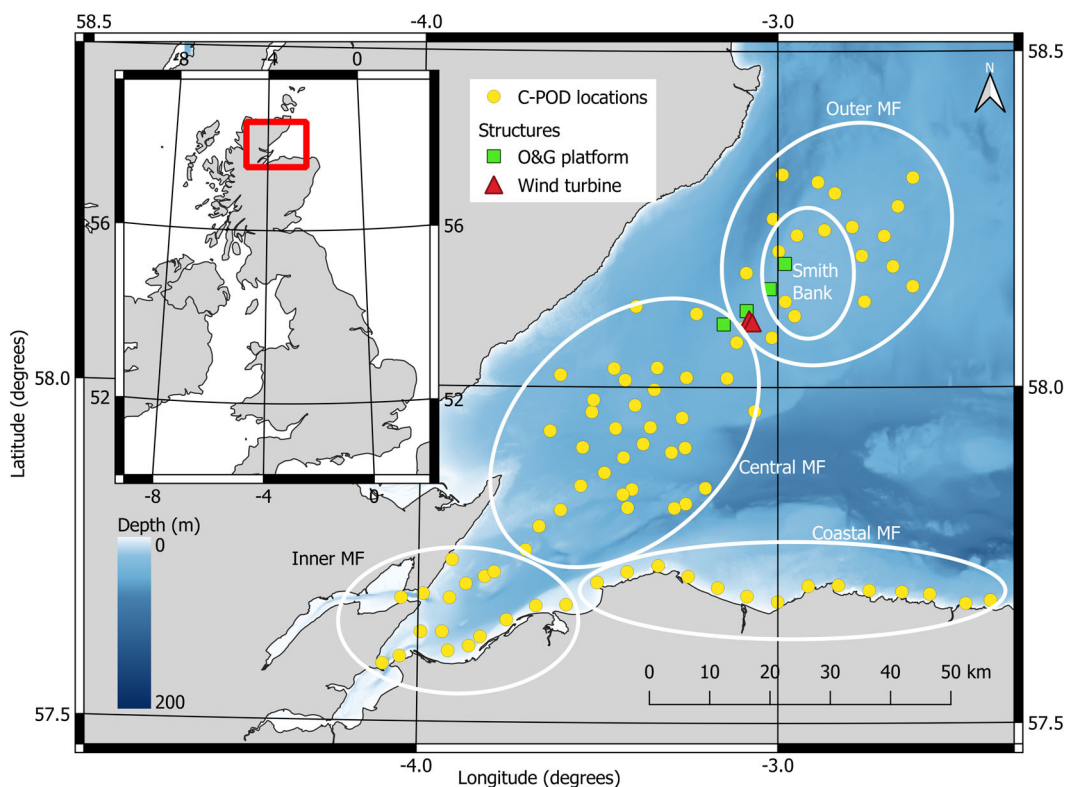


FIGURE 1 Locations of C-POD deployments used in analysis showing locations of outer, central, inner, and coastal portions of the Moray Firth (MF) and the Smith Bank. Inset shows the location of the Moray Firth in relation to the British Isles.

TABLE 1 Number of C-POD locations surveyed and the total number of hours of data each month.

Month	# locations surveyed	# hours of data
July 2009	51	11,076
August 2009	51	18,105
September 2009	48	18,346
October 2009	49	14,372
July 2010	49	8,899
August 2010	58	14,295
September 2010	50	14,079
October 2010	44	7,225
July 2011	44	12,507
August 2011	37	12,731
September 2011	33	10,793
October 2011	41	11,950

in high latitudes across months. The time of sunrise, for example, changed by over 4 hr between the beginning of July and the end of October and by 6 hr between the summer and winter solstices. The daylight variable represents time of day relative to sunrise and sunset.

TABLE 2 Summary of models fitted.

	Occurrence model	Foraging model
Model components	Daylight, hours to dolphin detection, and a spatiotemporal field including a monthly AR1 process.	Daylight, and a spatiotemporal field including a monthly AR1 process.
Response variable	Presence or absence of a porpoise detection at each C-POD location within an hour.	Presence or absence of an echolocation click classified as a foraging buzz at each C-POD location within each hour in which a porpoise was detected.
Scale of predicted result	Probability of occurrence of porpoise (P_O), with limits 0–1.	Probability of occurrence of foraging activity (P_F), with limits 0–1.

2.4 | Modeling

Both occurrence and foraging models were fitted in a Hierarchical Bayesian framework using INLA (Rue et al., 2009). To approximate continuous space, the SPDE approach (Lindgren et al., 2011) was used, which approximates the Gaussian field using a flexible stochastic model that is continuous in space (Blangiardo et al., 2013). The SPDE approach requires a triangulation mesh of the modeled area. The mesh provides a lower bound on the spatial resolution for analysis, and therefore a mesh should be developed which is fine enough so that no further changes in the results can be observed when a finer mesh is used (Lindgren et al., 2011). The triangulation mesh for the SPDE was created, bounded by the coastline with an inner (finer) mesh extending 10 km from C-POD locations and an outer mesh extending from 10 to 20 km from C-PODs. The outer mesh was used to prevent boundary effects and since it is outside the range of data, a coarser resolution can be used for computational efficiency. The mesh generator was allowed to place vertices randomly as needed with a maximum edge length of 4 km between vertices in the inner mesh and 10 km in the outer mesh. A minimum angle of 25° and a minimum edge length of 2 km were permitted. The SPDE was specified using penalized complexity (PC)-priors (Simpson et al., 2017) guiding the spatial range and standard deviation of the Matérn covariance function used in the Gaussian field approximation. These priors informed the model that the minimum spatial range was likely to be 3 km, with a likely maximum standard deviation of 2.

In both models, the Gaussian field specification was grouped into distinct time points (months), to enable the discretization of the sampling region over time. These spatiotemporal fields incorporated an autoregressive (AR1) process as the temporal function, capturing temporal correlation between consecutive months. This enabled the spatial distribution of the response variables to be estimated for each month of data (July–October 2009–2011), while accounting for temporal correlation.

Both daylight and hours to dolphin detection exhibited complex nonlinear relationships with the response variables. To capture these effects, they were modeled using the SPDE approach with each explanatory variable modeled as Matérn functions related to one-dimensional meshes based on the range of each variable (e.g., 0 to 1 for daylight). Incorporating the explanatory variables in this way revealed the nonlinear features of the effects and enabled the inclusion of this complexity in the overall models. This enabled inclusion of the effect of these variables on the spatial distribution of porpoise occurrence and foraging activity, while simultaneously capturing fine-scale temporal impact of these variables on the responses. For both occurrence and foraging models, a binomial distribution was used.

These models were then used to predict the probability of porpoise occurrence (P_O , occurrence model) and the probability of foraging activity (P_F , foraging model) on a scale between 0 and 1, onto the 2D spatial mesh, for each month of data (July–October 2009–2011). The relative widths of the 95% posterior credible interval (RWPCI), a measure of relative uncertainty (Yuan et al., 2017), for each model were also plotted and are shown in Figures S1

and S2. The effect of hours to dolphin detection and daylight on P_O and daylight on P_F were also predicted. The model of P_F failed to converge when hours to dolphin detection was included. Modeling smaller subsets of the data (i.e., each month separately) revealed that the relationship between hours to dolphin detection and P_F showed no effect (i.e., the relationship was a straight horizontal line). Hours to dolphin detection was therefore removed, and the model converged. To view how P_O and P_F were related to hours to dolphin detection and daylight in the different geographic areas, simpler models were run without the spatiotemporal field for each area (inner, coastal, central, and outer MF and Smith Bank). Theoretically, the full model should be able to include these spatial replicates; however, in practice, such a complex model was not computationally possible and had to be run as separate models. The mean results from 1,000 samples of these predictions were then plotted (Figures 2–6).

Code can be seen in Appendix S1 for both the occurrence and foraging models. Modeling was performed in R version 4.0.3 (R Core Team, 2020) using *inlabru* version 2.2.4.9000 (Bachl et al., 2019) and *INLA* version 20.03.17 (Rue et al., 2009).

3 | RESULTS

Between July and September each year, P_O was highest on Smith Bank in the outer MF (15–23 hr/day; Figure 2), but porpoise detections in this offshore area decreased in October to 10–12 hr/day (Figure 2 and Table 3). In the central MF, detection was moderate in 2009 and 2010, with 8–12 hr/day. Lower detection rates were generally recorded in the inner MF (1–5 hr/day; Table 3). Overall, sites along the south coast had detections of 9%–25% of hours but some coastal locations in the eastern part of the study area had higher detection (20 hr/day) throughout 2009 and July/August 2010. However, this area was not included in the array after August 2010, so the longer-term consistency of these patterns could not be evaluated (Table 3).

In contrast to the higher rates of overall detections at Smith Bank (47%–84% of hours), P_F was low in these areas compared to inner and coastal MF sites in 2009 and 2010, but similar in 2011 (Table 3). Harbor porpoises were detected most frequently (in 41% of surveyed hours) in offshore areas that had the lowest dolphin density (Table 3). However, harbor porpoise detections did still occur in coastal areas with higher bottlenose dolphin detection (7.6% of hours in inner MF area and 18.8% in coastal MF), suggesting that porpoises and dolphins may be interacting in these areas. Porpoise detections decreased 2–3 hr before dolphin detection in the inner MF, with the lowest detection 1 hr after dolphin detection, and returned to pre-dolphin levels 2–3 hr after (Figure 4). In the coastal MF, there was a strong decrease in porpoise detections when dolphins were detected; however, in central and offshore regions, there was no trend in porpoise vs. dolphin detections.

Porpoise occurrence in the inner and central MF was highest at night (Figure 5), while in the coastal and outer MF, detection was highest around sunrise, and detections were high throughout the day on the Smith Bank, with a decrease during the night. Foraging was detected more at night in all areas (Figure 6); however, P_F was highest generally in the coastal and inner MF.

4 | DISCUSSION

Harbor porpoise echolocation detection was explored in relation to fine-scale temporal drivers including detection of a potential competitor. We have shown that locations with the highest probability of porpoise foraging activity do not necessarily coincide with areas of highest probability of occurrence, and that probability of occurrence decreases prior to arrival of dolphins, which may (intentionally or not) result in avoidance of negative interactions at fine spatial scales.

These data show that harbor porpoises in the Moray Firth shifted their overall distribution between summer and autumn at a relatively fine spatial scale. Annual variation in prey movement may be a possible driver. Porpoise are

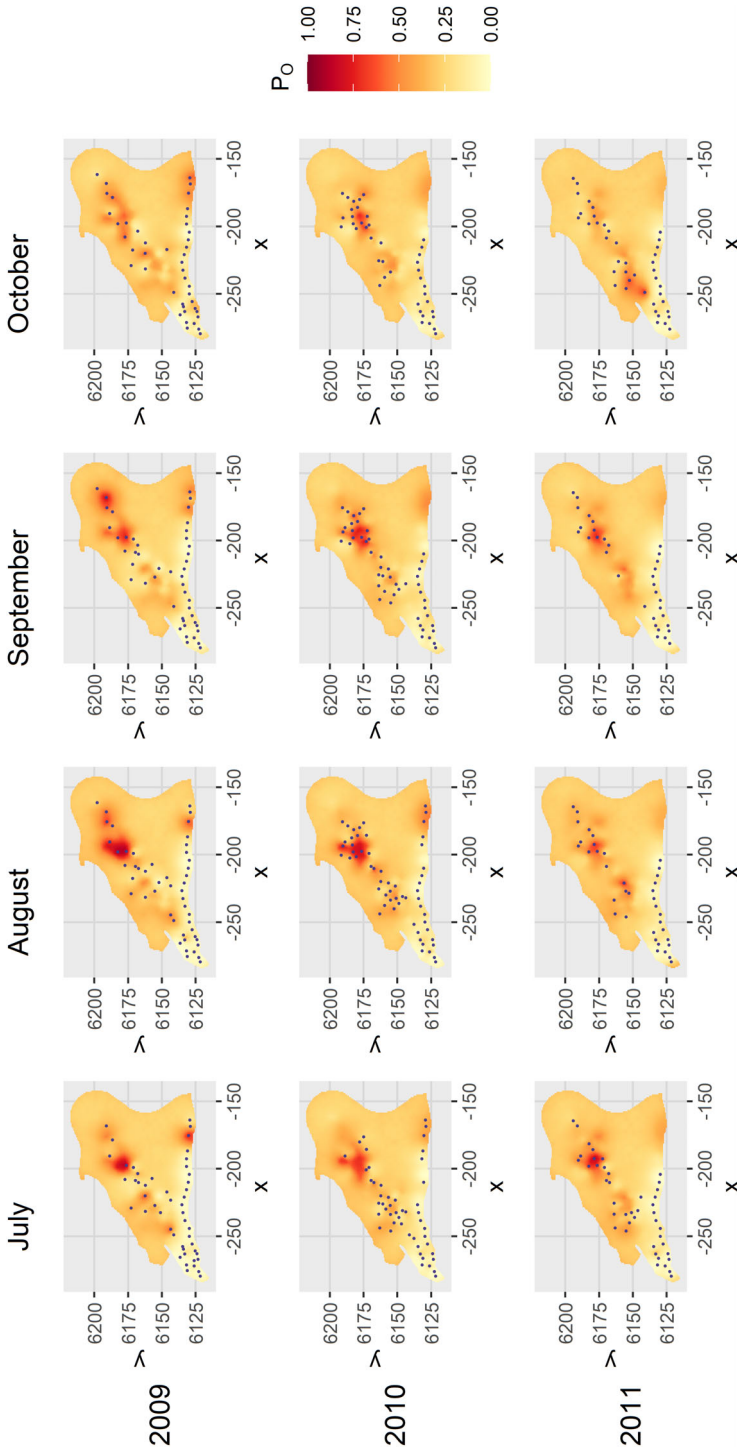


FIGURE 2 Probability of porpoise occurrence (P_o) in July–October 2009–2011. All figures are scaled from 0 to 1, indicating low to high probability. Blue points represent the locations of C-PODs deployed in that month.

TABLE 3 Percentage of the total number of hours of data for each area and month in which porpoise were detected (%DP of Total). Percentage of the number of hours of data in which porpoise were detected for which dolphins (%D of DP) and porpoise foraging buzzes (%F of DP) were also detected.

Month	Type	Area				
		Inner MF	Coastal MF	Central MF	Outer MF	Smith Bank
July 2009	%DP of Total	5.24	14.47	35.32	39.08	56.21
	%D of DP	7.01	4.85	1.35	1.26	3.16
	%F of DP	33.58	49.19	25.68	26.05	3.16
August 2009	%DP of Total	7.96	16.78	31.5	52.05	84.06
	%D of DP	9.16	3.72	1.94	2.36	2.41
	%F of DP	39.32	44.93	25.16	38.85	0.69
September 2009	%DP of Total	9.55	20.09	29.03	51.23	69.65
	%D of DP	5.91	4.57	1.48	2.88	3.43
	%F of DP	36.52	45.05	21.48	43.72	1.78
October 2009	%DP of Total	19.63	25.34	41.91	41.3	57.49
	%D of DP	4.79	4.86	4.39	2.35	3.01
	%F of DP	50.68	54.94	42.98	32.55	0
July 2010	%DP of Total	7.97	17.12	38.5	44.63	52.08
	%D of DP	9.06	4.23	1.44	1.46	0
	%F of DP	44.53	41.63	39.46	36.5	20
August 2010	%DP of Total	13.56	14.48	43.31	48.64	68.32
	%D of DP	8.04	3.68	2.29	1.79	2.18
	%F of DP	45.14	38.81	43.51	32.14	23.27
September 2010	%DP of Total	14.39	19.54	38.76	48.73	60.83
	%D of DP	6.24	3.29	2.46	2.25	3.31
	%F of DP	40.65	46.2	39.8	31.28	31.46
October 2010	%DP of Total	11.09	18.51	37.9	40.13	55.43
	%D of DP	6.05	4.15	2.97	2.03	2.68
	%F of DP	21.37	44.81	25.25	23.76	25.21
July 2011	%DP of Total	9.86	9.15	38.44	47.32	61.29
	%D of DP	6.43	2.09	2.85	2.31	4.77
	%F of DP	38.96	34.29	20.73	26	45.61
August 2011	%DP of Total	10.98	12.5	57.14	48.32	59.02
	%D of DP	5.28	4.07	2.38	1.86	1.85
	%F of DP	40	31.67	28.57	25.52	43.83
September 2011	%DP of Total	7.43	12.41	29.29	38.72	65.72
	%D of DP	2.14	5.26	1.72	2.96	2.43
	%F of DP	35.94	32.35	25.86	38.52	51.89
October 2011	%DP of Total	12.39	15.07	50.38	35.78	47.78
	%D of DP	3.81	3.55	1.52	2.56	4.15
	%F of DP	46.69	45.9	42.59	32.4	42.09

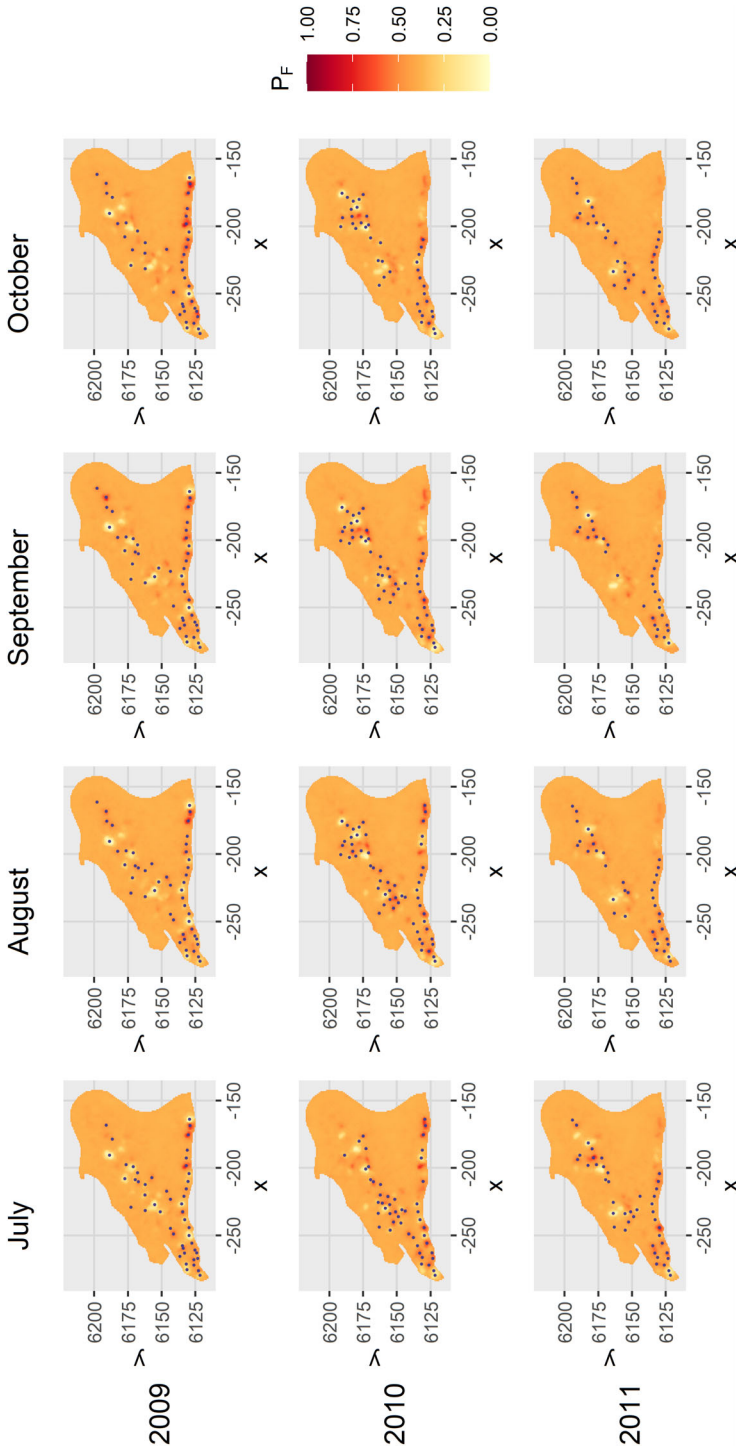


FIGURE 3 Probability of porpoise foraging activity (P_F) in July-October 2009-2011. All figures are scaled from 0 to 1, indicating low to high probability. Blue points represent the locations of C-PODs deployed in that month. Areas distant from C-PODs show P_F of about 0.5—this is due to a lack of information; therefore, the model selects the average between 0 and 1.

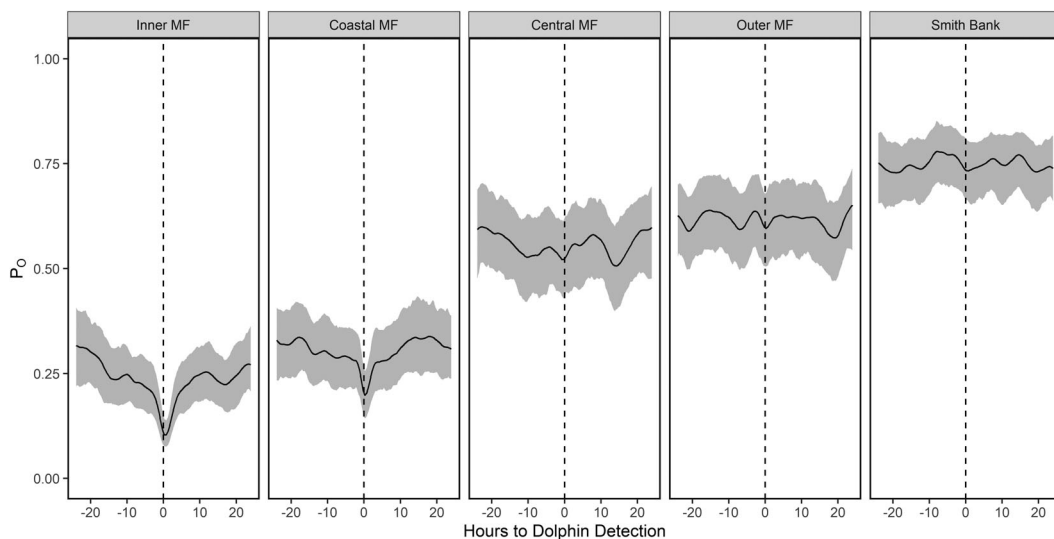


FIGURE 4 Effect of hours to dolphin detection on probability of porpoise occurrence (P_O) in each area. Negative values of hours are before dolphins are detected and positive are after. The dotted line at zero shows the hour in which dolphins were detected.

known to exhibit seasonal movements in some areas (e.g., Gilles et al., 2016; Nuuttila et al., 2017; Schaffeld et al., 2016) and observed shifts in distribution between months are often considered to be related to prey availability (Gilles et al., 2016) because harbor porpoises have a high metabolic rate and need to eat frequently to sustain themselves (Jones et al., 2014; Santos et al., 2004; Wisniewska et al., 2016).

The overall distribution of harbor porpoises, P_O (Figure 2), differed markedly from spatial patterns in P_F (Figure 3). It is important to note, that the P_F recorded here is the probability of detecting a foraging buzz, not necessarily the probability of a porpoise actually buzzing. Areas with highest P_F were generally in the inner and central MF (Figure 3).

Observed differences between P_O and P_F (Figures 2 and 3) may be influenced by a variety of drivers. Porpoises may use different foraging strategies (potentially targeting different prey species) in different habitats. It is possible that different foraging behaviors are not equally detectable by the C-PODs (e.g., bottom grubbing versus pelagic foraging); in addition, depth of deployment may impact detections, with previous studies reporting that C-PODs moored higher in the water column detect more porpoises (Alonso & Nuuttila, 2014). In the current study, C-PODs were moored 2–5 m above the seabed, below mid-water in depths that varied from 7–73 m. However, the shallowest inshore locations where C-PODs were moored relatively high within the water column were those where porpoise detections were lowest and dolphin detections highest. Thus, while there remains uncertainty over detection probabilities, known effects of depth on detection (Alonso & Nuuttila, 2014), do not appear to be driving the patterns we observed here.

Harbor porpoises may also exhibit behavioral changes in different areas based on competitor or predator species, making detection probability habitat specific. Studies using animal-borne recorders indicate that harbor porpoises' foraging buzzes are primarily produced either at the top or bottom of a dive (Linnenschmidt et al., 2013). If foraging using techniques such as bottom grubbing, where they target prey buried in the sediment, foraging clicks will be directed at the seabed (Schaffeld et al., 2016). Because echolocation clicks are highly directional and quiet, foraging behaviors such as bottom grubbing are less likely to be recorded by C-PODs (Akamatsu et al., 2005; Schaffeld et al., 2016). Sandeels are important prey for porpoises in the MF during summer (Santos & Pierce, 2003; Santos et al., 2004). Smith Bank had the highest probability of porpoise occurrence (Figure 2), and also provides good

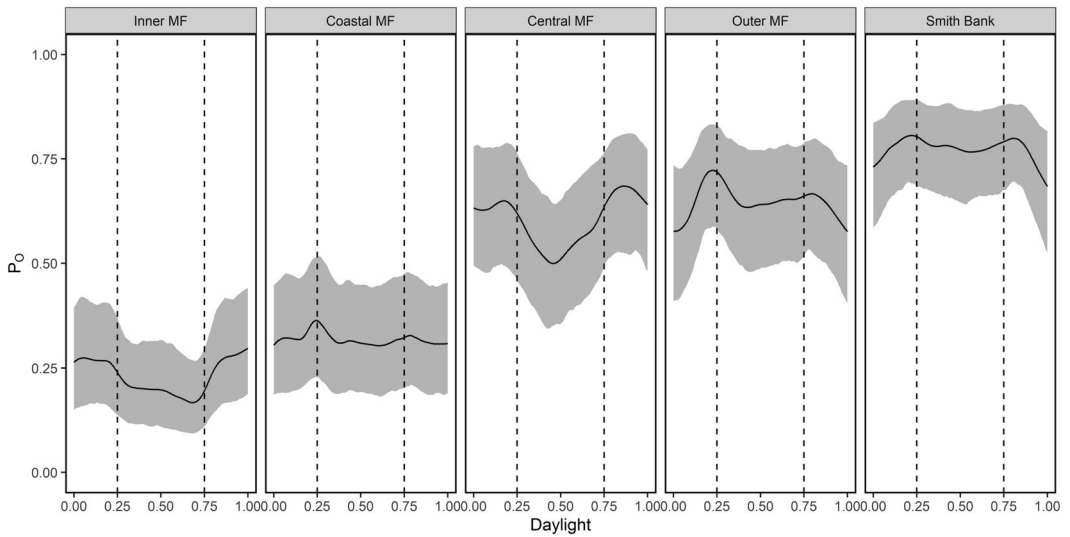


FIGURE 5 Effect of daylight on probability of porpoise occurrence (P_O) in each area. Daylight is bounded between 0 and 1, with dotted lines at 0.25 and 0.75 indicating sunrise and sunset, respectively.

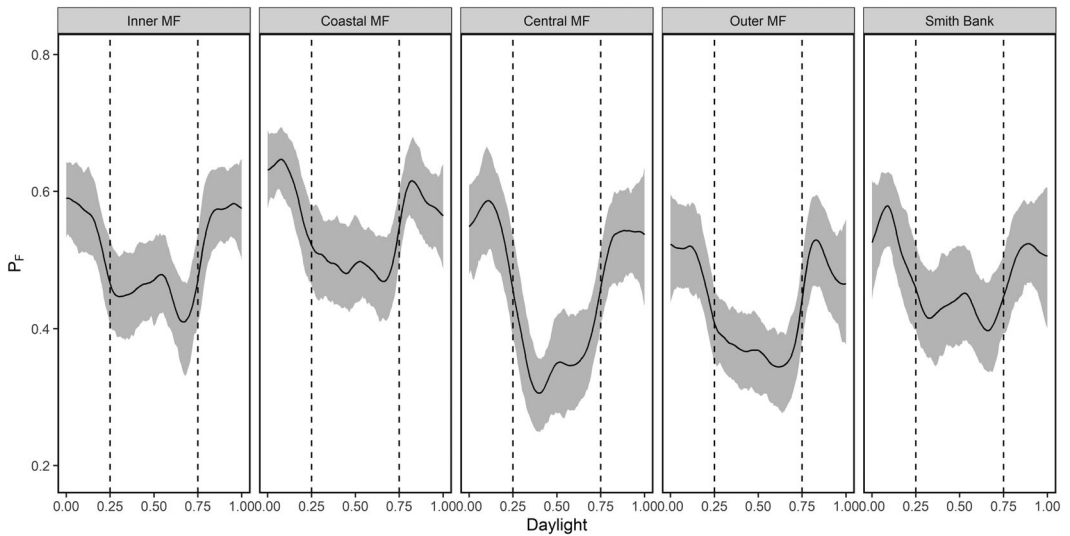


FIGURE 6 Effect of daylight on probability of porpoise foraging activity (P_F) in each area. Daylight is bounded between 0 and 1, with dotted lines at 0.25 and 0.75 indicating sunrise and sunset, respectively.

habitat for sandeels (Holland et al., 2005; Hopkins, 2011; Wright et al., 2000); however, a low P_F was recorded in this area (Figure 3 and Table 3). During summer, sandeels spend part of their time in the water column but bury themselves in the sediment at night (Winslade, 1974). Given current understanding of foraging patterns, it is unlikely that foraging clicks are detected by C-PODs if the clicks are directed toward the sediment and away from the hydrophones. Thus, methodological constraints mean that more focused studies are required to understand the mechanisms driving these patterns.

Another explanation for the higher P_F recorded in 2009–2010 in the inner MF is avoidance of competitors and predators. While porpoises have been reported to echolocate nearly continuously (Akamatsu et al., 2005; Au, 1993), they may either vocalize less in the inner MF, to minimize violent interactions with dolphins (resulting in lower observed occurrence), or may only enter the area at specific times to forage. It has been suggested that a similar vocal restriction to avoid predation by killer whales caused porpoises to develop high-frequency communication and abandon use of lower-frequency whistles in the first place (Morisaka & Connor, 2007).

Probability of porpoise occurrence was lowest 1 hr after dolphin clicks were detected by C-PODs in the inner MF. However, P_O decreased from 24 hr before dolphin detection, with decrease in detections greatest 2–3 hr prior to dolphin detection in the inner MF (Figure 4), suggesting that porpoises may anticipate arrival of dolphins. C-PODs only detect dolphins within approximately 1 km (Nuuttila et al., 2013) and previous estimates of the active space of bottlenose dolphins indicate that conspecifics can be detected at up to 20 km (Janik, 2000); therefore, it seems reasonable to assume that porpoises detect dolphin vocalizations at similar distances. Given a maximum swimming speed of 20.5 km/hr (Rohr et al., 2002), porpoises should therefore be able to detect approaching dolphins at least an hour before a C-POD; potentially much longer if dolphins are swimming more slowly or following an indirect path. Alternatively, porpoises may use other cues such as daylight or tidal variables to determine when dolphins are less likely to be present in particular sites, or the two species may simply be independently responding to different dynamic habitat variables within these sites that result in temporal segregation.

In offshore areas with low densities of dolphins, harbor porpoise occurrence was unrelated to dolphin detections, potentially a result of having few dolphin detections. Alternatively, it could be that offshore dolphin detections are most likely to be other species (Palmer et al., 2017; Thompson et al., 2014) such as common, white-beaked, or Risso's dolphins, which have not been reported to kill porpoise. Distribution of other predators, such as killer whales, white sharks, and gray seals (not known to kill harbor porpoise in this area) may also affect their distribution.

Trends between porpoise occurrence and daylight were similar to those observed by Williamson et al. (2017) in which porpoise were detected more during the night in muddy areas (corresponding to the Central MF) and more during the day in shallow sandy areas (e.g., the Smith Bank). This emphasizes that porpoise presence is also habitat specific. Foraging in all areas increased at nighttime, as has previously been reported (e.g., Brandt et al., 2014; Todd et al., 2009; Williamson et al., 2017).

Ultimately, disentangling drivers of these observed patterns in harbor porpoise distribution, foraging, and interactions with competitors and predators will require additional research (specifically on foraging strategies and prey targeted in different habitats); however, these trends play a vital role in an animal's use of space and can impact management options and potential interactions with offshore industries.

AUTHOR CONTRIBUTIONS

Laura Williamson: Conceptualization; formal analysis; investigation; methodology; writing-original draft; writing-review & editing. **Beth Scott:** Conceptualization; supervision; writing-review & editing. **Megan Laxton:** Formal analysis. **Fabian Bachl:** Software. **Janine Illian:** Supervision; writing-review & editing. **Kate Brookes:** Data curation; supervision. **Paul Thompson:** Conceptualization; data curation; project administration; supervision; writing-review & editing.

ORCID

Laura D. Williamson  <https://orcid.org/0000-0001-6026-9026>

Beth E. Scott  <https://orcid.org/0000-0001-5412-3952>

Megan R. Laxton  <https://orcid.org/0000-0002-5017-7395>

Janine B. Illian  <https://orcid.org/0000-0002-6130-2796>

Kate L. Brookes  <https://orcid.org/0000-0003-1376-4862>

Paul M. Thompson  <https://orcid.org/0000-0001-6195-3284>

REFERENCES

- Akamatsu, T., Wang, D., Wang, K., & Naito, Y. (2005). Biosonar behaviour of free-ranging porpoises. *Proceedings of the Royal Society B: Biological Sciences*, 272(1565), 797–801. <https://doi.org/10.1098/rspb.2004.3024>
- Alonso, M. S., & Nuuttila, H. K. (2014). Detection rates of wild harbour porpoises and bottlenose dolphins using static acoustic click loggers vary with depth. *Bioacoustics*, 24(2), 1–10. <https://doi.org/10.1080/09524622.2014.980319>
- Au, W. W. (1993). *The sonar of dolphins*. Springer Verlag.
- Bachl, F. E., Lindgren, F., Borchers, D. L., & Illian, J. B. (2019). inlabru: an R package for Bayesian spatial modelling from ecological survey data. *Methods in Ecology and Evolution*, 10(6), 760–766. <https://doi.org/10.1111/2041-210x.13168>
- Bailey, H., Clay, G., Coates, E. A., Lusseau, D., Senior, B., & Thompson, P. M. (2010). Using T-PODs to assess variations in the occurrence of coastal bottlenose dolphins and harbour porpoises. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 20(2), 150–158. <https://doi.org/10.1002/aqc.1060>
- Benoit-Bird, K. J., Battaile, B. C., Heppell, S. A., Hoover, B., Irons, D., Jones, N., Kuletz, K. J., Nordstrom, C. A., Paredes, R., Suryan, R. M., Waluk, C. M., & Trites, A. W. (2013). Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. *PLoS ONE*, 8(1), e53348. <https://doi.org/10.1371/journal.pone.0053348>
- Blangiardo, M., Cameletti, M., Baio, G., & Rue, H. (2013). Spatial and spatio-temporal models with R-INLA. *Spatial and Spatio-temporal Epidemiology*, 7, 39–55. <https://doi.org/10.1016/j.sste.2012.12.001>
- Brandt, M., 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*)? *Marine Mammal Science*, 30(3), 1109–1121. <https://doi.org/10.1111/mms.12112>
- 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. *Marine Ecology Progress Series*, 421, 205–216. <https://doi.org/10.3354/meps08888>
- Brookes, K. L., Bailey, H., & Thompson, P. M. (2013). Predictions from harbor porpoise habitat association models are confirmed by long-term passive acoustic monitoring. *Journal of the Acoustical Society of America*, 134(3), 2523–2533. <https://doi.org/10.1121/1.4816577>
- Carlström, J. (2005). Diel variation in echolocation of wild harbor porpoises. *Marine Mammal Science*, 21(1), 1–12. <https://doi.org/10.1111/j.1748-7692.2005.tb01204.x>
- Chelonia Ltd. (2014a). C-POD specification. https://www.chelonia.co.uk/cpod_specifications.htm
- Chelonia Ltd. (2014b). CPOD.exe: a guide for users. <https://www.chelonia.co.uk/downloads/CPOD.pdf>
- Dähne, M., Gilles, A., Lucke, K., Peschko, V., Adler, S., Krugel, K., Sundermeyer, J., & Siebert, U. (2013). Effects of pile-driving on harbour porpoises (*Phocoena phocoena*) at the first offshore wind farm in Germany. *Environmental Research Letters*, 8, 025002. <https://doi.org/10.1088/1748-9326/8/2/025002>
- De Boer, M. N., Simmonds, M. P., Reijnders, P. J. H., & Aarts, G. M. (2014). The influence of topographic and dynamic cyclic variables on the distribution of small cetaceans in a shallow coastal system. *PLoS ONE*, 9(1), e86331. <https://doi.org/10.1371/journal.pone.0086331>
- Dunn, D. C., Boustany, A. M., & Halpin, P. N. (2011). Spatio-temporal management of fisheries to reduce by-catch and increase fishing selectivity. *Fish and Fisheries*, 12(1), 110–119. <https://doi.org/10.1111/j.1467-2979.2010.00388.x>
- 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*). *Biological Conservation*, 143(2), 267–279. <https://doi.org/10.1016/j.biocon.2009.09.005>
- Fauchald, P. (2009). Spatial interaction between seabirds and prey: review and synthesis. *Marine Ecology Progress Series*, 391, 139–151. <https://www.int-res.com/abstracts/meps/v391/p139-151/>
- Gilles, A., Viquerat, S., Becker, E. A., Forney, K. A., Geelhoed, S. C. V., Haelters, J., Nabe-Nielsen, J., Scheidat, M., Siebert, U., Sveegaard, S., Van Beest, F. M., Van Bemmelen, R., & Aarts, G. (2016). Seasonal habitat-based density models for a marine top predator, the harbor porpoise, in a dynamic environment. *Ecosphere*, 7(6), e01367. <https://doi.org/10.1002/ecs2.1367>
- Graham, I. M., Merchant, N. D., Farcas, A., Barton, T. R., Cheney, B., Bono, S., & Thompson, P. M. (2019). Harbour porpoise responses to pile-driving diminish over time. *Royal Society Open Science*, 6(6), 190335. <https://doi.org/10.1098/rsos.190335>
- Hall, A. (2011). *Foraging behaviour and reproductive season habitat selection of northeast Pacific porpoises* [Doctoral dissertation]. University of British Columbia.
- Hammond, P. S., Berggren, P., Benke, H., Borchers, D. L., Collet, A., Heide-Jørgensen, M. P., Heimlich, S., Hiby, A. R., Leopold, M. F., & Øien, N. (2002). Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. *Journal of Applied Ecology*, 39(2), 361–376. <https://doi.org/10.1046/j.1365-2664.2002.00713.x>
- Hammond, P. S., Lacey, C., Gilles, A., Viquerat, S., Börjesson, P., Herr, H., Macleod, K., Ridoux, V., Santos, M. B., Scheidat, M., Teilmann, J., Vingada, J., & Øien, N. (2017). *Estimates of cetacean abundance in European Atlantic waters in summer 2016*

- from the SCANS-III aerial and shipboard surveys. <https://synergy.st-andrews.ac.uk/scans3/files/2017/04/SCANS-III-design-based-estimates-2017-04-28-final.pdf>
- Holland, G. J., Greenstreet, S. P. R., Gibb, I. M., Fraser, H. M., & Robertson, M. R. (2005). Identifying sandeel *Ammodytes marinus* sediment habitat preferences in the marine environment. *Marine Ecology Progress Series*, 303, 269–282. <https://doi.org/10.3354/meps303269>
- Hopkins, P. J. (2011). Exploited fish and shellfish species in the Moray Firth. *Proceedings of the Royal Society of Edinburgh, Section B: Biological Sciences*, 91, 57–72. <https://doi.org/10.1017/S026972700009234>
- Isojunno, S., Matthiopoulos, J., & Evans, P. G. H. (2012). Harbour porpoise habitat preferences: robust spatio-temporal inferences from opportunistic data. *Marine Ecology Progress Series*, 448, 155–170. <https://doi.org/10.3354/meps09415>
- Janik, V. (2000). Source levels and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland. *Journal of Comparative Physiology A*, 186(7–8), 673–680. <https://doi.org/10.1007/s003590000120>
- Jepson, P. D., & Baker, J. R. (1998). Bottlenosed dolphins (*Tursiops truncatus*) as a possible cause of acute traumatic injuries in porpoises (*Phocoena phocoena*). *Veterinary Record*, 143(22), 614–615. <https://doi.org/10.1136/vr.143.22.614>
- Johnston, D. W., Westgate, A. J., & Read, A. J. (2005). Effects of fine-scale oceanographic features on the distribution and movements of harbour porpoises *Phocoena phocoena* in the Bay of Fundy. *Marine Ecology Progress Series*, 295, 279–293. <https://www.int-res.com/abstracts/meps/v295/p279-293/>
- Jones, A. R., Hosegood, P., Wynn, R. B., De Boer, M. N., Butler-Cowdry, S., & Embling, C. B. (2014). Fine-scale hydrodynamics influence the spatio-temporal distribution of harbour porpoises at a coastal hotspot. *Progress in Oceanography*, 128, 30–48. <https://doi.org/10.1016/j.pocean.2014.08.002>
- Leopold, M. F., Begeman, L., Van Bleijswijk, J. D. L., IJsseldijk, L. L., Witte, H. J., & Gröne, A. (2015). Exposing the grey seal as a major predator of harbour porpoises. *Proceedings of the Royal Society B, Biological Sciences*, 282, 20142429. <https://doi.org/10.1098/rspb.2014.2429>
- Lindgren, F., Rue, H., & Lindström, J. (2011). An explicit link between Gaussian fields and Gaussian Markov random fields: the stochastic partial differential equation approach. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 73(4), 423–498. <https://doi.org/10.1111/j.1467-9868.2011.00777.x>
- Linnenschmidt, M., Teilmann, J., Akamatsu, T., Dietz, R., & Miller, L. A. (2013). Biosonar, dive, and foraging activity of satellite tracked harbor porpoises (*Phocoena phocoena*). *Marine Mammal Science*, 29(2), E77–E97. <https://doi.org/10.1111/j.1748-7692.2012.00592.x>
- MacLeod, C. D., Weir, C. R., Pierpoint, C., & Harland, E. J. (2007). The habitat preferences of marine mammals west of Scotland (UK). *Journal of the Marine Biological Association of the United Kingdom*, 87(01), 157–164. <https://doi.org/10.3354/meps10239>
- Marubini, F., Gimona, A., Evans, P. G. H., Wright, P. J., & Pierce, G. J. (2009). Habitat preferences and interannual variability in occurrence of the harbour porpoise *Phocoena phocoena* off northwest Scotland. *Marine Ecology Progress Series*, 381, 297–310. <https://doi.org/10.3354/meps07893>
- Morisaka, T., & Connor, R. C. (2007). Predation by killer whales (*Orcinus orca*) and the evolution of whistle loss and narrow-band high frequency clicks in odontocetes. *Journal of Evolutionary Biology*, 20(4), 1439–1458. <https://doi.org/10.1111/j.1420-9101.2007.01336.x>
- Nuuttila, H. K., Courteney-Jones, W., Baulch, S., Simon, M., & Evans, P. G. (2017). Don't forget the porpoise: acoustic monitoring reveals fine scale temporal variation between bottlenose dolphin and harbour porpoise in Cardigan Bay SAC. *Marine Biology*, 164(3), 50. <https://doi.org/10.1007/s00227-017-3081-5>
- Nuuttila, H. K., Thomas, L., Hiddink, J. G., Meier, R., Turner, J. R., Bennell, J. D., Tregenza, N. J. C., & Evans, P. G. H. (2013). Acoustic detection probability of bottlenose dolphins, *Tursiops truncatus*, with static acoustic dataloggers in Cardigan Bay, Wales. *Journal of the Acoustical Society of America*, 134(3), 2596–2609. <https://doi.org/10.1121/1.4816586>
- Palmer, K. J., Brookes, K., & Rendell, L. (2017). Categorizing click trains to increase taxonomic precision in echolocation click loggers. *Journal of the Acoustical Society of America*, 142(2), 863–877. <https://doi.org/10.1121/1.4996000>
- Patterson, I. A. P., Reid, R. J., Wilson, B., Grellier, K., Ross, H. M., & Thompson, P. M. (1998). Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbour porpoises? *Proceedings of the Royal Society B: Biological Sciences*, 265(1402), 1167–1170. <https://doi.org/10.1098/rspb.1998.0414>
- Philpott, E. (2013). *Examining potential effects of marine renewable energy developments on top predators* [Doctoral dissertation]. University of Aberdeen.
- Pirotta, E., Brookes, K. L., Graham, I. M., & Thompson, P. M. (2014). Variation in harbour porpoise activity in response to seismic survey noise. *Biology Letters*, 10(5). <https://doi.org/10.1098/rsbl.2013.1090>, 20131090
- Pompa, S., Ehrlich, P. R., & Ceballos, G. (2011). Global distribution and conservation of marine mammals. *Proceedings of the National Academy of Sciences of the United States of America*, 108(33), 13600–13605. <https://doi.org/10.1073/pnas.1101525108>

- R Core Team. (2020). *R: A language and environment for statistical computing* (Version. 4.0.3) [Computer software]. R Foundation for Statistical Computing.
- Read, A. J. (1999). The harbour porpoise *Phocoena phocoena* (Linnaeus, 1758). In S. H. Ridgeway & S. R. Harrison (Eds.), *Handbook of marine mammals* (Vol. 6, pp. 323–355). Academic Press.
- Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, 12(9), 982–998. <https://doi.org/10.1111/j.1461-0248.2009.01347.x>
- Rohr, J. J., Fish, F. E., & Gilpatrick, J. W., Jr. (2002). Maximum swim speeds of captive and free-ranging delphinids: Critical analysis of extraordinary performance. *Marine Mammal Science*, 18(1), 1–19. <https://doi.org/10.1111/j.1748-7692.2002.tb01014.x>
- Ross, H. M., & Wilson, B. (1996). Violent interactions between bottlenose dolphins and harbour porpoises. *Proceedings of the Royal Society of London B: Biological Sciences*, 263(1368), 283–286. <https://doi.org/10.1098/rspb.1996.0043>
- Rue, H., Martino, S., & Chopin, N. (2009). Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 71(2), 319–392. <https://doi.org/10.1111/j.1467-9868.2008.00700.x>
- Santos, M. B., & Pierce, G. J. (2003). The diet of harbour porpoise (*Phocoena phocoena*) in the northeast Atlantic. *Oceanography and Marine Biology: An Annual Review*, 41, 355–390.
- Santos, M. B., Pierce, G. J., Learmonth, J. A., Reid, R. J., Ross, H. M., Patterson, I. A. P., Reid, D. G., & Beare, D. (2004). Variability in the diet of harbor porpoises (*Phocoena phocoena*) in Scottish waters 1992–2003. *Marine Mammal Science*, 20(1), 1–27. <https://doi.org/10.1111/j.1748-7692.2004.tb01138.x>
- Schaffeld, T., Bräger, S., Gallus, A., Dähne, M., Krügel, K., Herrmann, A., Jabbusch, M., Ruf, T., Verfuß, U. K., & Benke, H. (2016). Diel and seasonal patterns in acoustic presence and foraging behaviour of free-ranging harbour porpoises. *Marine Ecology Progress Series*, 547, 257–272. <https://doi.org/10.3354/meps11627>
- Simpson, D., Rue, H., Riebler, A., Martins, T. G., & Sørbye, S. H. (2017). Penalising model component complexity: A principled, practical approach to constructing priors. *Statistical Science*, 32, 1–28. <https://doi.org/10.1214/16-ST5576>
- Skov, H., & Thomsen, F. (2008). Resolving fine-scale spatio-temporal dynamics in the harbour porpoise *Phocoena phocoena*. *Marine Ecology Progress Series*, 373, 173–186. <https://doi.org/10.3354/meps07666>
- Thompson, P. M., Brookes, K. L., & Cordes, L. S. (2014). Integrating passive acoustic and visual data to model spatial patterns of occurrence in coastal dolphins. *ICES Journal of Marine Science*, 72(2), 651–660. <https://doi.org/10.1093/icesjms/fsu110>
- Thompson, P. O., & White, S. (2004). Co-variation in the probabilities of sighting harbor porpoises and bottlenose dolphins. *Marine Mammal Science*, 20(2), 322–328. <https://doi.org/10.1111/j.1748-7692.2004.tb01160.x>
- Todd, V. L. G., Pearse, W. D., Tregenza, N. C., & Todd, I. B. (2009). Diel echolocation activity of harbour porpoises (*Phocoena phocoena*) around North Sea offshore gas installations. *ICES Journal of Marine Science*, 66, 734–745. <https://doi.org/10.1093/icesjms/fsp035>
- Verfuß, U. K., Miller, L. A., Pilz, P. K. D., & Schnitzler, H.-U. (2009). Echolocation by two foraging harbour porpoises (*Phocoena phocoena*). *Journal of Experimental Biology*, 212, 823–834. <https://doi.org/10.1242/jeb.022137>
- Waggitt, J. J., Evans, P. G. H., Andrade, J., Banks, A. N., Boisseau, O., Bolton, M., Bradbury, G., Breton, T., Camphuysen, C. J., Durinck, J., Felce, T., Fijn, R. C., Garcia-Baron, I., Garthe, S., Geelhoed, S. C. V., Gilles, A., Goodall, M., Haelters, J., Hamilton, S., ... Hiddink, J. G. (2020). Distribution maps of cetacean and seabird populations in the North-East Atlantic. *Journal of Applied Ecology*, 57(2), 253–269. <https://doi.org/10.1111/1365-2664.13525>
- 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 in Ecology and Evolution*, 7(7), 762–769. <https://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. *Marine Ecology Progress Series*, 570, 223–232. <https://doi.org/10.3354/meps12118>
- Wilson, B., Benjamins, S., & Elliott, J. (2013). Using drifting passive echolocation loggers to study harbour porpoises in tidal-stream habitats. *Endangered Species Research*, 22, 125–143. <https://doi.org/10.3354/esr00538>
- Wingfield, J. E., O'Brien, M., Lyubchich, V., Roberts, J. J., Halpin, P. N., Rice, A. N., & Bailey, H. (2017). Year-round spatiotemporal distribution of harbour porpoises within and around the Maryland wind energy area. *PLoS ONE*, 12(5), e0176653. <https://doi.org/10.1371/journal.pone.0176653>
- Winslade, P. (1974). Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt). II. The effect of light intensity on activity. *Journal of Fish Biology*, 6, 577–586. <https://doi.org/10.1111/j.1095-8649.1974.tb05101.x>
- Wirsing, A. J., Heithaus, M. R., Frid, A., & Dill, L. M. (2008). Seascales of fear: Evaluating sublethal predator effects experienced and generated by marine mammals. *Marine Mammal Science*, 24(1), 1–15. <https://doi.org/10.1111/j.1748-7692.2007.00167.x>

- Wisniewska, Danuta M., Johnson, M., Teilmann, J., Rojano-Doñate, L., Shearer, J., Sveegaard, S., Miller, Lee A., Siebert, U., & Madsen, Peter T. (2016). Ultra-high foraging rates of harbor porpoises make them vulnerable to anthropogenic disturbance. *Current Biology*, 26, 1–6. <https://doi.org/10.1016/j.cub.2016.03.069>
- Wright, P. J., Jensen, H., & Tuck, I. (2000). The influence of sediment type on the distribution of the lesser sandeel, *Ammodytes marinus*. *Journal of Sea Research*, 44(3), 243–256. [https://doi.org/10.1016/S1385-1101\(00\)00050-2](https://doi.org/10.1016/S1385-1101(00)00050-2)
- Yuan, Y., Bachl, F. E., Lindgren, F., Borchers, D. L., Illian, J. B., Buckland, S. T., Rue, H., & Gerrodette, T. (2017). Point process models for spatio-temporal distance sampling data from a large-scale survey of blue whales. *Annals of Applied Statistics*, 11(4), 2270–2297. <https://doi.org/10.1214/17-AOAS1078>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Williamson, L. D., Scott, B. E., Laxton, M. R., Bachl, F. E., Illian, J. B., Brookes, K. L., & Thompson, P. M. (2022). Spatiotemporal variation in harbor porpoise distribution and foraging across a landscape of fear. *Marine Mammal Science*, 38(1), 42–57. <https://doi.org/10.1111/mms.12839>