Vol. 708: 143–161, 2023 https://doi.org/10.3354/meps14268

Published March 23





Micro-scale spatial preference and temporal cyclicity linked to foraging in harbour porpoises

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ABSTRACT: Habitat heterogeneity is a crucial driver for species distribution across scales. Harbour porpoise *Phocoena phocoena* basin-wide distribution is linked to prey availability, and smallscale (kilometres to tens of kilometres) differences in distribution are prevalent. However, information on porpoise distribution and foraging-behaviour variations on a micro-scale (~100 m to kilometres) is limited. To monitor harbour porpoise distribution and foraging activity on a microscale, we deployed passive acoustic dataloggers, logging porpoise acoustic activity at 6 sites in a small, high porpoise-density area in southern Sweden. Data were collected for almost a year, giving detailed time series on porpoise activity. The time series were analysed using dynamic time warping to compare activity patterns between sites. Large differences were found between sites separated by only a few hundred meters, indicating micro-scale spatial preference. Spectral analysis for temporal cyclicity in activity revealed a dominant peak for 24 h cycles with higher activity at night for all sites. All sites also had a second peak for 29.5 d, linked to the lunar cycle with higher activity during full moon. Activity was overall highest during autumn and winter (September–December). Spatial and temporal patterns were linked to foraging, showing a positive correlation between porpoise presence and the percent of time present with detected foraging. The study demonstrates that harbour porpoise spatial distribution on a micro-scale should be considered in e.g. behavioural, management and conservation studies and actions. In addition, we show that time series statistical methodology is informative and appropriate for analysis of acoustic temporal data.

KEY WORDS: Distribution \cdot Foraging \cdot Harbour porpoise \cdot Passive acoustic monitoring \cdot Spatio-temporal \cdot Time series analysis

1. INTRODUCTION

Habitat heterogeneity is the result of spatial and temporal variation in physical and biological factors, which creates a mosaic of encountered environmental quality for individuals and populations (Barry & Dayton 1991). As such, habitat heterogeneity is fundamental in shaping ecosystem structure and species

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distribution in both marine and terrestrial ecosystems. The ability of species and individuals to adjust their distribution and behaviour in space and time, on both larger and finer scales, is beneficial since it allows optimized use of resources while reducing the risk of predation, which varies over both space and time (Stevick et al. 2002, Stephens et al. 2007). Most species are therefore not uniformly dispersed within

Publisher: Inter-Research · www.int-res.com

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their range of distribution, but instead aggregate spatio-temporally within certain areas which are often referred to as 'hotspots' (Myers 1988, Davoren 2013).

Animal aggregations at foraging hotspots are likely based on individual foraging decisions made in response to environmental cues (Stephens & Krebs 1986, Russell et al. 1992, Jones et al. 2014). For predators, a relationship between environmental cues and target prey species makes favourable foraging areas predictable as they signal the likelihood of encountering prey. Important environmental cues can be static and dynamic biological and physical variables, such as oceanographic features and hydrodynamics (e.g. Swartzman 1994, Thompson et al. 2012, Jones et al. 2014) or cyclic changes in abiotic factors resulting in regular and recurrent variations in prey availability (e.g. Womble & Sigler 2006, Sveegaard et al. 2012b). Understanding patterns in predator distribution, density and behaviour requires knowledge on how they interact with their environment, including prey, at a range of spatio-temporal scales (Fauchald & Erikstad 2002, Embling et al. 2012). For species that need conservation, such as the harbour porpoise Phocoena phocoena, this is especially important since it allows development of efficient conservation actions (Jones et al. 2014, Pirotta et al. 2014, Gilles et al. 2016).

The harbour porpoise is one of the smallest and most widely spread of the toothed whales, with a distribution covering coastal waters across the northern hemisphere (Read 1999). The porpoise's small size and high metabolic rate requires a high and frequent rate of feeding (Wisniewska et al. 2016, Rojano-Doñate et al. 2018). The distribution and abundance of harbour porpoises is therefore strongly influenced by the availability and distribution of their prey (Sveegaard et al. 2012a,b, Lawrence et al. 2016). Harbour porpoises feed on a variety of small benthic and pelagic fish, although their diet is often dominated by a few species (Aarefjord et al. 1995, Börjesson et al. 2003, Santos & Pierce 2003, Andreasen et al. 2017).

Some harbour porpoises seasonally travel over hundreds to thousands of kilometres, presumably between foraging and reproduction habitats (Johnston et al. 2005, Sveegaard et al. 2011b, Carlén et al. 2018, Nielsen et al. 2018). In addition, for shorter periods of time, they sometimes remain in more restricted areas and move over much shorter distances (kilometres to tens of kilometres) (Johnston et al. 2005, Teilmann et al. 2022). The spatial distribution of porpoises is uneven on scales finer than tens of kilometres, most likely reflecting a corresponding fine-scale spatial distribution of suitable prey driven by oceanographic features (Booth et al. 2013, Brandt et al. 2014, Williamson et al. 2022). For example, large water movements can result in aggregations of prey, which in turn attract marine predators (Alldredge & Hamner 1980, Wolanski & Hamner 1988). Therefore, regions where currents meet, like headlands and reefs with steep slopes or areas with strong tidal forces, sometimes represent important habitats for harbour porpoises (Johnston et al. 2005, Pierpoint 2008, Skov & Thomsen 2008, Isojunno et al. 2012, Jones et al. 2014, IJsseldijk et al. 2015). On a fine temporal scale, differences in porpoise activity show links to the diel cycle (e.g. Carlström 2005, Schaffeld et al. 2016, Wisniewska et al. 2016, Benjamins et al. 2017) and lunar cycle (Brennecke et al. 2021). These temporal patterns have been argued to reflect prey availability and light-dependent differences in the interactions between porpoises and prey, although a recent study on captive porpoises found the diel activity patterns to be independent of prey activity (Osiecka et al. 2020).

Opportunistic mobile predators, such as the harbour porpoise, can be expected to adapt their distribution and behaviour to prey availability and specific foraging scenarios. This allows them to move between foraging hotspots and target diverse prey resources (Stephens et al. 2007), and thereby optimize their foraging efficiency over varying scales. In this study we take advantage of the fact that harbour porpoises almost continuously emit high-frequency clicks to navigate, forage and communicate (Verfuß et al. 2005, Villadsgaard et al. 2007, Clausen et al. 2011, Amundin et al. 2022), and use passive acoustic monitoring data to investigate patterns in harbour porpoise presence and foraging. We do this on a spatial micro-scale, ranging from hundreds of meters up to a few kilometres, as well as on a temporal scale, ranging from diel phases to seasons. We also examine the connection between harbour porpoise presence and foraging, with the aim of investigating if prey availability is potentially driving porpoise presence within the study area. We analyse the data applying dynamic time warping and spectral methodology, which are widely used in time series data analysis, but represent a novel approach for passive acoustic monitoring studies.

2. MATERIALS AND METHODS

2.1. Study area

The Kullen peninsula is an accentuated mountain ridge located on the west coast of southern Sweden

at the northern inlet to Öresund, the sound between Denmark and Sweden (Fig. 1a). The narrow (3.5-40 km) and shallow (\leq 50 m) sound has a sill with a maximum depth of only 10 m in the south and is characterized by the meeting of salt water from the Skagerrak/North Sea (20-25‰) with brackish water from the Baltic Sea (7–10‰). Consequently, Öresund is stratified into 2 layers of water; a high-salinity bottom layer with a predominant southward current direction and a low-salinity surface layer with a predominant northward current direction (Wändahl 1980). The meeting of water bodies also generates a frontal area, with frequent downwelling events, especially at the tip of the Kullen headland, where there are strong currents (up to 5 knots) (SMHI 2021), zones of convergence and eddies, as well as oxygenated water and high nutrient concentrations (Wolanski & Hamner 1988, Myrberg & Andrejev 2003). Changes in sea level amplitude are stochastic and dominated by weather events primarily driven by changes in air pressure (causing amplitude changes over 1 m), while the tidal amplitude is only a few centimetres (SMHI 2014).

The northern parts of Öresund, including the Kullen area, is a key habitat for harbour porpoises *Phocoena phocoena* belonging to the Belt Sea population. Adults and pairs of mothers and calves are frequently encountered around Kullen during

the reproductive season in summer (Teilmann et al. 2008, 2022, Sveegaard et al. 2011a,b, J. Stedt pers. obs.). Anthropogenic activities in the Kullen area include small-scale fishing with static nets, the passing of a commercial shipping lane less than 1 km from the headland area, and recreational boat traffic.

2.2. Logging harbour porpoise activity

2.2.1. Passive acoustic monitoring using C-PODs

The acoustic activity of harbour porpoises was continuously logged at 6 sites in the study area from April 2014 to March 2015 using autonomous passive acoustic data loggers (continuous-porpoise detectors, also known as C-PODs; Chelonia Ltd.). The duration of the time series of data collected varied between the survey sites due to differences in battery life of the C-PODs. The survey sites were located along the coastline, stretching from the tip of Kullen and along the northern side of the peninsula, at different bottom substrates (Fig. 1b). The depth at the 6 survey sites ranged from 14 to 30 m (Site 1: 30 m, Site 2: 28 m, Site 3: 22 m, Site 4: 25 m, Site 5: 20 m, Site 6: 14 m). A minimum of 700 m was kept between survey sites to eliminate the risk of simultaneous detection of the



Fig. 1. Location and details of study area. (a) Study area, with (b) survey sites (Sites 1–6) and data on bottom substrate, along the coast of the Kullen peninsula in the northern part of Öresund, the sound between Denmark and Sweden

same porpoise click event on multiple C-PODs. At each survey site, a C-POD was anchored with the hydrophone approximately 2 m above the seabed, following standard procedure for porpoise studies. All C-PODs were retrieved and serviced (change of batteries and memory cards) at least once during the entire survey period and then re-deployed a few hours or days later. To distribute potential instrumental variation individual C-PODs were rotated between sites (Table S1 in the Supplement at www.int-res.com/articles/suppl/m708p143_supp. pdf).

A C-POD is a self-contained archival data logger consisting of a hydrophone and electronics with a user-controlled firmware designed to detect and log a number of parameters of echolocation clicks of toothed whales. Data are saved on an SD card and uploaded upon retrieval of the C-POD. Using digital waveform analysis, the C-POD selects and logs cetacean click events in the frequency range of 20-160 kHz, including their time of occurrence, duration (5 µs resolution), amplitude, bandwidth and centre frequency (Chelonia Ltd. 2015). C-POD detection ranges for harbour porpoise clicks vary depending on environmental conditions but are typically considered to be approximately 200-300 m (Chelonia Ltd. 2014, Amundin et al. 2022). Even within this range, only a smaller proportion of all clicks are detected (Amundin et al. 2022) due to the directionality of the beam of harbour porpoise clicks (Koblitz et al. 2012). However, due to the high vocalization rate of harbour porpoises (Wisniewska et al. 2016, Amundin et al. 2022), a porpoise passing within the C-POD's detection range is still likely to be detected.

All C-PODs used in this study were calibrated in a circular wooden tank at the SDU Marine Biological Centre in Kerteminde, Denmark, prior to deployment to make sure that their detection thresholds were comparable. In these calibrations, porpoise-like clicks were transmitted in 31 trains of 10 clicks, each click containing 13 cycles of 130 kHz contained in a raised cosine envelope (Verfuß et al. 2013). The peak-peak amplitude was reduced by 1 dB from one train to the next. By rotating each C-POD, the threshold was measured at 4 angles of incidence (0°, 90°, 180° and 270°) around the omnidirectional hydrophone in the horizontal plane. The sound level was measured using a calibrated Reson TC4014 hydrophone connected via a custom-built amplifier to an oscilloscope and deployed prior to the C-POD measurements at the site of the C-POD hydrophone. By knowing the initial sound level of the first train (137 dB re 1 µPa pp at 1 m), the sound level threshold for each C-POD

and angle could be established as the sound level at which 50% of the clicks were detected (Dähne et al. 2013b). The variation in mean detection threshold of the C-PODs used were in the range of ± 3 dB (Table S1), which was considered an acceptable inter-instrumental variation (Dähne et al. 2013b).

2.2.2. Data extraction

All C-POD data were analysed using the CPOD.exe software v. 2.044 (Chelonia Ltd.). The 'KERNO' classifier was used to identify the characteristic narrowband high-frequency (NBHF) click trains produced by harbour porpoises. For the click train classification, KERNO uses several numerical descriptors of click trains, including click centre frequency, bandwidth, duration, and inter-click interval. Using standard procedure for porpoise studies (e.g. Brandt et al. 2014, Benjamins et al. 2017, Zein et al. 2019), only click trains assigned to the NBHF category with the 2 highest levels of probability ('Hi' and 'Mod') were extracted and used in the subsequent analysis.

The click train data from each logger were extracted as a text file from CPOD.exe and truncated by at least 1 h from deployment or retrieval of the C-POD, to exclude data influenced by the deployment/ retrieval process. The text files were then imported into Matlab (ver. 2013a, MathWorks Inc.) and transformed (according to variable descriptions below) into site-specific matrices containing (1) time, given as date and hour, (2) porpoise presence, given as detection positive minutes h^{-1} (DPM h^{-1} , range 0–60), (3) percent of time present with detected foraging, given as foraging-to-presence percentage (FPP, range 0-100%; see definition below), (4) hour of day, (5) lunar phase and (6) month. All data were presented as UTC+1, which is the standard time in Sweden (not using daylight saving time).

To create full time series for all survey sites, all missing values for hours when C-PODs were serviced (representing 0.7% of the data) were assigned with substituted values using imputation. Imputation is a prediction of a missing data point based on a general context/pattern from neighbouring data points. Imputation is often done to satisfy assumptions of statistical methods. Several different imputation strategies were tested and visually evaluated before identifying seasonally decomposed missing value imputation from the 'imputeTS' package (Moritz & Bartz-Beielstein 2017) in R version 4.1.1 (R Core Team 2021) as the strategy providing highest resemblance of imputed values to surrounding data.

2.3. Indicators of harbour porpoise activity

Two different indicators of harbour porpoise acoustic activity were used:

2.3.1. Detection positive minutes (DPM) h⁻¹, representing porpoise presence

A DPM is defined as a minute during which at least 1 porpoise click train — consisting of at least 5 consecutive clicks with a maximum inter-click-interval (ICI) of around 250 ms — has been detected according to the predefined criteria used by C-POD.exe. Consequently, DPM is a binary measure which only gives porpoise detection (1) or no detection (0) in a given minute. DPM is one of the most frequently used variables when analysing harbour porpoise presence using passive acoustic monitoring (PAM, e.g. C-PODs) and the raw binary data is often transformed into continuous data and given as the proportion of DPM per given unit of time (e.g. Simon et al. 2010, Williamson et al. 2016, Benjamins et al. 2017). In this study the variable DPM h^{-1} (range 0–60), describing the number of minutes in a given hour during which at least 1 porpoise click train is detected, was calculated and used as a measure of porpoise presence.

2.3.2. Foraging-to-presence percentage (FPP), representing foraging

The proportion of DPM h⁻¹ that included acoustic foraging behaviour was calculated as a modified version of the term feeding buzz ratio (modified from Todd et al. 2009). Foraging was identified in the acoustic data by identification of so-called foraging buzzes. A foraging 'buzz' was defined as at least 5 consecutive clicks with an ICI of <10 ms (Carlström 2005, Todd et al. 2009, Zein et al. 2019) and used as a proxy for foraging behaviour. This measure is based on the observation that harbour porpoises decrease the ICI to <10 ms during prey capture attempts (Verfuß et al. 2009). While searching for prey or navigating, the ICI normally varies between 30 and 100 ms, but when locked on a target fish the ICI becomes progressively shorter as the porpoise approaches the prey, sometimes down to 1 ms when the prey is only a few meters away (Koschinski et al. 2008, Verfuß et al. 2009, Miller & Wahlberg 2013). High-repetition rate click trains are also produced by porpoises while communicating, but the majority of click trains with high-repetition rates are buzzes associated with foraging (Sørensen et al. 2018). A buzz positive minute (BPM) was defined as a minute with at least 1 buzz (Zein et al. 2019). The raw BPM is thus, like DPM, a binary measure giving foraging detection (1) or no detection (0) in a given minute. The variable FPP was calculated as the ratio of BPMs to DPMs in each hour and multiplied by 100 to provide it as a percentage:

$$FPP = \left(\frac{BPM}{DPM}\right) \times 100 \tag{1}$$

The variable FPP (range 0–100%) represents a proxy for the percentage of time harbour porpoises spend foraging while at a survey site, and it was used as a measure of foraging.

2.4. Temporal classification

All data were finally given 3 different temporal classifications: (1) hour of day, (2) lunar phase and (3) month. The classification into lunar phase was made using lunar illumination data from NASA (https:// svs.gsfc.nasa.gov/4955). All data were classified into 1 of 8 lunar phases (new, waxing crescent, first quarter, waxing gibbous, full, waning gibbous, third quarter, waning crescent) based on the lunar illumination value and illumination progress (increasing/ decreasing illuminated surface; for definitions see Fig. S1 in the Supplement).

2.5. Statistical analysis

All statistical analysis was performed on both variables of porpoise activity (DPM h^{-1} and FPP) using R version 4.1.1 (R Core Team 2021).

2.5.1. Spatial analysis

Similarities in DPM h^{-1} and FPP patterns between survey sites were investigated using dynamic time warping (DTW). In time series analysis, DTW is widely used for pair-wise comparison of individual time series as it provides a normalized distance measure, which is insensitive to local compression and stretches of the times series, reflecting the similarity or dissimilarity of compared time series (Berndt & Clifford 1994, Giorgino 2009). Other standard distance metrics that are not specific to time series, such as Euclidean distance, are not appropriate to use for establishing relations between time series trajectories as they assume independence of all data points. In contrast, DTW takes into account that data points in a time series trajectory are typically correlated, i.e. not independent, as there is some sort of 'memory' propagating between the data points. In this way, DTW pays attention to the overall shape of the trajectories rather than comparing the time series point-by-point with each other. For that reason, DTW has been demonstrated to be optimal for discovering similarities in shapes of time series trajectories (Bagnall et al. 2017).

Raw time series trajectories typically represent a complex mixture of periodic patterns and stochastic noise. Therefore, prior to DTW analysis, all hourly data for both variables and 6 survey sites were smoothened using simple moving average. We used a moving average in a sliding window strategy and examined a wide range of possible window sizes. A window size of 14 d was empirically determined as representing a good balance between over- and underfitting the time series trajectories. A risk of using too small window size, i.e. overfitting, is that the downstream analysis can potentially become too sensitive to the noise, while a large window size, i.e. underfitting, can potentially lead to removal of seasonal oscillations of interest.

DTW analysis was then carried out for both variables and all possible pairs of survey sites using the 'dtw' package in R (Giorgino 2009) with a symmetric step pattern. Normalized DTW distances for all pairwise time series comparisons were extracted into a distance matrix to investigate similarities and dissimilarities between survey sites. This was done using hierarchical cluster analysis with complete linkage method. Finally, identified clusters were plotted as dendrograms, using the 'ggtree' package in R (Yu 2020), to visualize hierarchical similarities between survey sites.

2.5.2. Temporal analyses

Temporal patterns were investigated separately for each time series, i.e. variable and survey site. Presence of both high frequency cyclicity (short periods, e.g. diel cyclicity) and low frequency cyclicity (long periods, e.g. lunar cyclicity) were analysed using spectral analysis. In spectral analysis, data are transformed from the time domain into the frequency domain using Fourier transform, allowing subsequent analysis for presence and strength of periodic components of a signal at different frequencies.

Spectral analysis was performed on detrended time series. Detrending of time series data refers to the removal of potential changes in the mean value over time, with the purpose of removing a potentially distorting aspect from the data, and satisfy underlying assumptions of the spectral analysis. In this study, detrending was done before investigating potential periodic frequencies to remove an overall monotonic change over time that can mask the presence of periodic signals. The computed trend was subtracted from the raw time series. More specifically, detrending was performed using a moving average of 24 h for investigation of high frequency cyclicity. For investigation of low frequency cyclicity, detrending was performed on the time series already smoothened over 14 d using a moving average of 30 d.

Using the function 'spectrum' in the 'stats' package in R (R Core Team 2021), the periodogram for each detrended time series was calculated and plotted against frequency, with the frequency axis converted to cycles per unit time. Each periodogram was visually inspected to identify detected peaks, which were several magnitudes higher than, and clearly distinguished from, noise in the periodograms. For each periodogram and time series, the dominant cyclic component (peak) and any other strong cyclic patterns were identified, using the 'photobiology' package in R (Aphalo 2015). The peak search within 'photobiology' was performed by spline interpolation of data points in each periodogram with the consequent identification of local maxima present in the interpolated curve. The local maxima (peaks) for each periodogram and time series were extracted into a matrix and used to calculate the mean frequency \pm SD of detected dominant cyclic components.

Boxplots were computed to visualize the distribution of detected cyclic components in the low and high frequency range, respectively. This was done using the matrix with data on local maxima for each periodogram and time series. Boxplots were also created to investigate the shape of the cyclic components, i.e. to determine at what time DPM h^{-1} and FPP was highest or lowest. This was done using the full time series, including the imputed values for the servicing periods, for all survey sites.

Monthly differences in DPM h⁻¹ and FPP could not be analysed using spectral analysis, as this requires a longer time series covering repeated monthly cycles. Instead, differences between months were investigated using boxplots.

2.5.3. Correlation between presence (DPM h^{-1}) and foraging (FPP)

The relation between DPM h^{-1} and FPP was analysed separately for each survey site with the Spear-

man rank correlation test using the function 'cor.test' in the 'stats' package in R (R Core Team 2021). The results were visualized in scatter plots using the function 'ggscatter' in the 'ggpubr' package in R (Kassambara 2020). In addition, cross-correlation plots were computed using the function 'ccf' in the 'stats' package in R (R Core Team 2021) to provide an in-depth visualization of correlation between the curves at different lags. This was done to address the strong temporal linkage (autocorrelation) between corresponding data points in 2 time series curves. The cross-correlation is calculated by gradual shifting (lagging) of one time series curve with respect to the other and computing a correlation between the shifted curves at each lag.

3. RESULTS

3.1. Data availability

The mean recording time for the 6 survey sites was 303 d, minimum 240 d (Site 2) and maximum 342 d (Site 4), from April 2014 to March 2015.

3.2. Spatial differences

There were large differences in both harbour porpoise *Phocoena phocoena* presence (DPM h^{-1}) and foraging (FPP) for some survey sites, while for other survey sites there were more similar activity levels (Fig. 2, Table 1). Site 1 had the highest DPM h^{-1} and FPP, followed by Sites 2, 3 and 4 with relatively intermediate DPM h^{-1} and FPP, and Sites 5 and 6 with the lowest DPM h^{-1} and FPP (Fig. 2).

From the cluster analysis, based on normalized pairwise DTW distances (Table 1), it was reasonable, and verifiable from visual inspection of the time series data, to conclude the presence of 3 main clusters: Site 1 formed one cluster, Sites 2, 3 and 4 formed a second cluster, and Sites 5 and 6 formed a third cluster (dendrograms in Fig. 2). Normalized DTW distances were used for relative comparisons between pairs of time series from different survey sites, with a low distance value indicating that the pair of time series have similar patterns, and a high distance value indicating that the pair of time series 5 and 6 had very low distance values (Table 1) and strong clustering structures (dendrograms in Fig. 2), indicating almost identical patterns of DPM h^{-1} and FPP.

The large branching heights in the dendrograms at which the cluster with Sites 5 and 6 separates from

the other survey sites reflects that DPM h^{-1} and FPP at these 2 survey sites were very different from the other survey sites. Sites 3 and 4 also had almost identical patterns in DPM h^{-1} and FPP, with almost as strong clustering structures as Sites 5 and 6. At Sites 3 and 4, DPM h^{-1} and FPP was similar to Site 2, but this result must be interpreted with caution as the time series at Site 2 was about 3 mo shorter than those at Sites 3 and 4.

The dendrograms for DPM h⁻¹ and FPP are almost identical and show the same spatial pattern (dendrograms in Fig. 2). This pattern, with the same 3 clusters of data and a striking similarity between the 2 variables, is also very distinct in the time series plots (Fig. 2). It is also clear from the time series plots (Fig. 2) that Site 1 had a much higher DPM h^{-1} and FPP and periodically opposing pattern than the rest of the survey sites. In fact, DPM h⁻¹ and FPP at Site 1 was, for the majority of the study period, 2 to 4 times higher than that at the rest of the survey sites. In comparison, Sites 2, 3 and 4 had medium to high levels of DPM h⁻¹ and FPP for most of the time, while Sites 5 and 6 displayed much lower levels. There were, however, periods during the autumn and winter (October–December), when the DPM h⁻¹ and FPP at Sites 2-6 matched or even exceeded that of Site 1.

3.3. Temporal patterns

There were strong cyclic components detected in the high and low frequency range for both variables and all 6 survey sites, correlated to diel and lunar cyclicity, respectively.

3.3.1. High frequency range: diel cyclicity

In the high frequency range, there was a very strong and dominant cyclic component with a frequency representing a diel pattern over 24 h for both variables and all survey sites (Table 2, Fig. 3). For some of the survey sites there were also other cyclic components, representing patterns over 12 and 8 h, several magnitudes weaker and less consistent than the diel pattern. When investigating the shape of the diel cyclicity, it was clear that both DPM h^{-1} and FPP were highest at night, with peaks around midnight, and lowest during the day (Fig. 4). Like the time series plots (Fig. 2), the diel cyclicity plots also show clear spatial differences between survey sites. The overall highest levels of DPM h^{-1} and FPP was found at Site 1, followed by Sites 2, 3 and 4, which had



Fig. 2. Time series plots and dendrograms from cluster analysis. Time series plots for both variables: (a) presence (detection positive minutes, DPM h⁻¹, 0–60) and (b) foraging (foraging-to-presence percentage, FPP, %), and all survey sites (Sites 1–6). Note that scales on the *y*-axes are different. Dendrograms show results from cluster analysis based on normalized distances from dynamic time warping (DTW)-analysis (Table 1). Height of the dendrogram (x-axis) reflects the distance of the clusters, i.e. clusters separated at a larger height are less similar than clusters separated at a lower height

Table 1. Normalized distance matrix from dynamic time warping (DTW)-analysis. Normalized distances for all pairwise comparisons between the 6 survey sites (Sites 1–6) in DTW-analysis on time-series representing presence (detection positive minutes, DPM h^{-1}) and foraging (foraging-to-presence percentage, FPP)

Survey site	1	2	3	4	5	6
Presence (DPM h ⁻¹)						
1		_	_	_	_	_
2	1.99		_	_	_	_
3	2.34	0.87		_	_	_
4	1.90	1.19	0.36		_	_
5	5.85	1.60	1.43	1.49		_
6	5.67	2.34	1.90	2.20	0.37	
Foraging (FPP)						
1		_	_	_	_	_
2	1.61		_	_	_	_
3	2.20	0.78		_	_	_
4	2.13	1.26	0.46		_	_
5	6.85	2.88	2.01	2.99		_
6	8.61	4.58	3.35	4.31	0.35	

DPM h^{-1} and FPP levels similar to each other but at a lower level than Site 1, and the lowest levels of DPM h^{-1} and FPP at Sites 5 and 6. In addition, the plots revealed a complete lack of FPP (i.e. foraging) during daytime at Site 6 (Fig. 4b).

3.3.2. Low frequency range: lunar cyclicity

In the low frequency range, cyclic patterns over 22–42 d could be detected for both response variables and all survey sites (Table 3). All detected cyclicities clearly overlapped with a periodic component representing a complete lunar cycle of 29.5 d (Fig. 5). There was an indication of somewhat higher DPM h^{-1} and FPP during full moon at most of the survey sites (Fig. S2 in the Supplement). Similarly, DPM h^{-1} and FPP appear to be lowest during the phases adjacent to full moon, i.e. waning and waxing gibbous as well as third and first quarter. However, the variation within lunar cycle and survey site was large, making it difficult to interpret cyclic patterns.

3.3.3. Monthly differences

Large differences between different periods of the year were found in both variables, with a generally higher DPM h^{-1} and FPP at all survey sites during the autumn and winter (in particular September–

Table 2. Temporal cyclicity in the high frequency range. Detected dominant cyclic component (h, mean \pm SD) in the high frequency range from spectral analysis for both variables: presence (detection positive minutes, DPM h⁻¹) and foraging (foraging-to-presence percentage, FPP) and all survey sites (Sites 1–6)

Site	— Cyclic component Presence (DPM h ⁻¹)	(mean h ± SD) — Foraging (FPP)
1	24.0 ± 0.6	24.0 ± 0.0
2	24.1 ± 0.5	23.8 ± 0.3
3	24.0 ± 0.0	24.0 ± 0.0
4	24.3 ± 0.3	24.0 ± 0.0
5	24.0 ± 0.3	23.8 ± 0.3
6	24.5 ± 0.3	24.1 ± 0.5

December) than during the rest of the year (Fig. 6). In terms of periods with lower activity, the variation between variables and survey sites was greater, but for some survey sites (e.g. Sites 1 and 2) there was a clear period with much lower DPM h^{-1} and FPP during the spring (April–May). For Sites 5 and 6, there was an interesting pattern with an almost complete lack of FPP during all months except during the autumn and winter (September–December) when the FPP suddenly became relatively high (Fig. 6b). In



Fig. 3. Temporal cyclicity in the high frequency range. Detected dominant cyclic component (h) from spectral analysis for presence (detection positive minutes, DPM h^{-1} , 0–60) and foraging (foraging-to-presence percentage, FPP, %), and all survey sites (Sites 1–6). Lower and upper box boundaries: 25th and 75th percentiles; lower and upper error lines: 10th and 90th percentiles. Black line inside each box: median value. Dotted line: diel cyclicity (cyclic component of 24 h)



Fig. 4. Diel differences. Harbour porpoise activity for each hour of the day for both variables: (a) presence (detection positive minutes, DPM h⁻¹, 0–60) and (b) foraging (foraging-to-presence percentage, FPP, %), and all survey sites (Sites 1–6). Lower and upper box boundaries: 25th and 75th percentiles; lower and upper error lines: 10th and 90th percentiles. Black line inside each box: median value. Scales on the *y*-axes are different

Table 3. Temporal cyclicity in the low frequency range. Detected dominant cyclic component (d, mean \pm SD) in the low frequency range from spectral analysis for both variables: presence (detection positive minutes, DPM h⁻¹) and foraging (foraging-to-presence percentage, FPP) and all survey sites (Sites 1–6)

Site	— Cyclic component (Presence (DPM h ⁻¹)	(mean d ± SD) — Foraging (FPP)
1	22.0 ± 14.9	24.7 ± 15.1
2	22.9 ± 11.3	20.8 ± 11.2
3	24.1 ± 15.0	36.5 ± 9.1
4	32.7 ± 18.4	32.4 ± 5.1
5	34.1 ± 19.6	42.1 ± 16.2
6	29.0 ± 7.6	29.0 ± 7.6

general, the shape of the patterns in DPM h^{-1} and FPP at Sites 2–6 was very similar throughout the entire survey period. At Site 1, however, the patterns in DPM h^{-1} and FPP were somewhat different, with overall stable and high levels during all surveyed months, except during the spring (April–May) when they were distinctively lower.

3.4. Correlation between presence (DPM h⁻¹) and foraging (FPP)

A significant positive correlation between DPM h⁻¹ and FPP was found for all survey sites (Table 4; rho 0.69–0.75; Fig. S3). The correlation was significant for almost all lags (Fig. S4), providing additional support for a strong correlation between DPM h⁻¹ and FPP. In addition, the cross-correlation plots confirm the periodic signal in the DPM h⁻¹ and FPP time series data as it has a clear maximum of correlation at lag = 24 h (Fig. S4). This implies that the temporal periodic pattern reflected by the correlations between DPM h⁻¹ and FPP is repeated every 24 h.

4. DISCUSSION

4.1. Micro-scale spatial preference

The results from this study demonstrate that the acoustic activity of harbour porpoises *Phocoena phocoena*, measured as both presence (DPM h^{-1}) and foraging (FPP), can vary considerably and consistently over a fine spatial scale (hundreds of meters to a few kilometres). At these micro-scales we could identify 3 spatial clusters for both DPM h^{-1} and FPP (dendrograms in Fig. 2).

The survey sites were distributed between the 3 clusters so that it also reflected their distance to the tip of the Kullen headland. Lowest DPM h⁻¹ and FPP was found at the highly distinctive cluster formed by Sites 5 and 6 (Fig. 2), located furthest from the tip of the Kullen headland. These 2 sites, separated by 1.5 km, had almost identical patterns in DPM h^{-1} and FPP, which were very different from the patterns at the other survey sites. The second highly distinctive cluster was formed by Sites 2, 3 and 4. The distance between any 2 of these 3 survey sites varies between less than 1 km to up to 2 km (Fig. 1). Like Sites 5 and 6, these 3 survey sites had almost identical patterns in DPM h⁻¹ and FPP. Highest DPM h⁻¹ and FPP was found at Site 1 at the tip of the Kullen headland. This survey site represented a third distinctive cluster, with levels of DPM h⁻¹ and FPP that often were several times higher than those at the other survey sites (Fig. 2). This was particularly striking as Site 1 is located only about 700 m from Site 2.

The differences in DPM h^{-1} and PPM between clusters could perhaps be linked to differences in depth and bottom substrate, as these variables differ between the tip of the Kullen headland (max depth: 30 m, substrate: mud) and the area surrounding Sites



Fig. 5. Temporal cyclicity in the low frequency range. Detected dominant cyclic component (d) from spectral analysis for presence (detection positive minutes, DPM h^{-1} , 0–60) and foraging (foraging-to-presence percentage, FPP, %), and all survey sites (Sites 1–6). Lower and upper box boundaries: 25th and 75th percentiles; lower and upper error lines: 10th and 90th percentiles. Black dot: outlier. Black line inside each box: median value. Dotted line: lunar cyclicity (cyclic component of 29.5 d)



Fig. 6. Monthly differences. Harbour porpoise activity for the different months of a year for both variables: (a) presence (detection positive minutes, DPM h^{-1} , 0–60) and (b) foraging (foraging-to-presence percentage, FPP, %), and all survey sites (Sites 1–6). Boxplots for some of the months and stations are missing because of lack of data. Lower and upper box boundaries: 25th and 75th percentiles; lower and upper error lines: 10th and 90th percentiles. Black line inside each box: median value. Scales on the y-axes are different

Table 4. Results from Spearman's rank correlation test between presence (detection positive minutes, DPM h^{-1}) and foraging (foraging-to-presence percentage, FPP). Spearman p-value and Spearman correlation coefficient (rho) for each survey site (Sites 1–6). Asterisks indicate statistical significance

Site	p-value	Correlation coefficient (rho)
1	< 0.0001***	0.75
2	< 0.0001***	0.69
3	< 0.0001***	0.73
4	< 0.0001***	0.72
5	< 0.0001***	0.71
6	< 0.0001***	0.75

5 and 6 (max depth: 20 m, substrate: sand and gravel). The Kullen headland area is, given its position at the inlet to Öresund, probably also characterized by more intense water movements, including stronger currents and frontal zones. These environmental cues can be used by predators as signals of spatial predictability of prey. They may also indicate to porpoises that this is an area with increased likelihood of encountering prey. Feeding in distinctive areas has also been hypothesized to be a beneficial foraging strategy for porpoises as it reduces their need for movement between foraging patches (Skov & Thomsen 2008). As such, the Kullen headland area could represent a favourable foraging location and distinct micro-scale hotspot for harbour porpoises within the already identified important key habitat around the Kullen peninsula in the northern part of Oresund (Teilmann et al. 2008, 2022, Sveegaard et al. 2011a,b). Contrary to what might be expected based on the high acoustic activity levels at Site 1, this site is most subjected to potential disturbance from boat traffic (including both recreational and commercial vessels).

4.2. Link between porpoise presence and foraging

Predator density is known to be closely linked to prey density (Carbone & Gittleman 2002). In this study this is reflected in the strong correlation (Table 4, Fig. S3) and cross-correlation (Fig. S4) between DPM h^{-1} and FPP. These 2 variables have almost identical patterns and the same clustering structure (Fig. 2), demonstrating that the presence of harbour porpoises is a strong indicator of an area's importance for foraging. The most plausible explanation for the positive correlation between DPM h^{-1} and FPP (Table 4) is that porpoise presence was driven by foraging opportunities. As FPP is calculated as a proportion of DPM h⁻¹, the positive correlation shows that harbour porpoises spend more time in areas with good foraging opportunity and use a higher proportion of the time foraging when being there. Conversely, in areas where porpoises are detected to a lesser extent of the time, they also spend a smaller proportion of the time present foraging. We interpret this as porpoise presence being driven by foraging opportunities. This relates well to the metabolic needs of harbour porpoises which force them to forage frequently (Wisniewska et al. 2016, Rojano-Doñate et al. 2018). The link between DPM h⁻¹ and FPP suggests that the micro-scale spatial heterogeneity within the study area was most likely caused by variations in foraging opportunities for harbour porpoises and that Site 1 is undoubtedly the most important foraging site for harbour porpoises within the study area.

4.3. Seasonal differences

Two general conclusions can be made from the overall patterns in DPM h⁻¹ and FPP for the different survey sites over the course of the full time series. First, Site 1 seems to be an important foraging habitat for harbour porpoises almost independently of season, with the only possible exception being late April and May when DPM h⁻¹ and FPP is relatively lower (Fig. 6). Second, the remaining 5 sites are of less importance for all months except October-December (Fig. 6). This seasonal increase in porpoise presence was especially noticeable for Sites 5 and 6 (Fig. 6a), and together with Sites 3 and 4 these 2 survey sites also showed the most pronounced seasonal variation in foraging activity (Fig. 6b). In fact, Sites 5 and 6 displayed a shift from being practically unused as foraging areas to guite high FPP during October–December. Interestingly, the peak in FPP at Site 6 in December is followed by a drastic decline in January, down to levels representing an almost complete lack of foraging (Fig. 6b). The seasonal use of the rather shallow bottoms with sand and gravel at Site 5 and 6 might indicate seasonal variation in availability or quality of prey, or that porpoises were targeting a different prey species. It is also likely that the increase in FPP reflects the higher food intake of harbour porpoises during late summer and autumn (mid-July to November/December) (Rojano-Doñate et al. 2018, Gallagher et al. 2021) and a corresponding increase in foraging rates during this time of year.

Harbour porpoises have high metabolic costs of living correlating with a high diet quality need (Spitz et al. 2012). One of the most important prey species for harbour porpoises in the study area, both with regard to energy content and proportion of the diet, is Atlantic herring *Clupea harengus* (Börjesson et al. 2003, Sveegaard et al. 2012a, Andreasen et al. 2017). The Rügen spring spawning stock of herring overwinters in the Öresund area between August and February (Nielsen et al. 2001). Consequently, the presence of large numbers of herring might explain the high porpoise presence and foraging activity during the winter months, and perhaps also the high DPM h^{-1} and FPP observed at Sites 5 and 6 in October– December.

On the population level, the best available data on spatio-temporal distributional patterns of Belt Sea harbour porpoises are based on individual movement data from satellite transmitters (Sveegaard et al. 2011b, Teilmann et al. 2022). These studies have shown that harbour porpoises are present in the northern part of Öresund and at Kullen mainly during March-November, with the highest abundance during spring and summer (March-August). Harbour porpoises have also been suggested to increase their acoustic activity during the mating season in the summer (Osiecka et al. 2020), which could be misinterpreted as an increased true presence if acoustic methods are used. Our results, however, reveal a completely opposing pattern for most of our survey sites (Sites 2-6) with the lowest levels of activity during spring and summer (March–August) and highest porpoise presence during October-December (Figs. 2 & 6). A likely explanation to this is the difference in scales. The time period for this study is much shorter since it only includes approximately 1 yr of data (2014-2015), while the satellite studies are based on data collected over almost 25 yr (1997-2021). Also, the spatial scales differ by several orders of magnitude, with this study focusing on spatio-temporal patterns over hundreds of meters to a few kilometres in a very limited area, while the satellite studies investigate movement patterns and distribution over a much larger spatial scale. As a strong spatial correlation has been found between large-scale acoustic detections using a towed hydrophone array and density distribution from satellite tagged porpoises (Sveegaard et al. 2011a), the difference is not likely due to the different survey platforms. Rather it shows that satellite data provide us with representative general distribution patterns, while stationary acoustic monitoring is more suitable for studies of small-scale spatio-temporal heterogeneity and detection of microscale hotspot areas, such as the one at the Kullen headland area.

4.4. Diel cyclicity

The identification of a very strong and distinct periodic component over 24 h for both variables and all 6 survey sites (Table 2, Fig. 3) demonstrates the presence of diel cyclicity in harbour porpoise activity. The same periodic component over 24 h was found in the cross-correlation between DPM h⁻¹ and FPP, providing further support for presence of diel cyclicity (Fig. S4). In line with previous studies (e.g. Carlström 2005, Todd et al. 2009, Schaffeld et al. 2016, Wisniewska et al. 2016, Benjamins et al. 2017), DPM h⁻¹ was highest at night, with peaks around midnight, and lowest during the day (Fig. 4). The diel cyclicity in harbour porpoise presence has been proposed to be linked to increased foraging during nighttime, probably reflecting a higher availability of prey or diel differences in prey behaviour causing a higher echolocation rate (e.g. Todd et al. 2009, Brandt et al. 2014, Schaffeld et al. 2016). Also, harbour porpoises have higher respiration rates at night (Rojano-Doñate et al. 2018), which fits well with a nocturnal increase in foraging activity (Wisniewska et al. 2016).

The strong correlation between DPM h⁻¹ and FPP (Table 4) supports the hypothesis that the increase in acoustic detections at night is linked to an increase in foraging-associated acoustic activity. As such, it indicates that foraging behaviour is indeed a driver for the diel activity pattern in free-ranging harbour porpoises, although this was refuted in a recent study on captive porpoises (Osiecka et al. 2020). The captive porpoises were considered to be largely unaffected by the presence of wild prey as they were provided sufficient food to cover their metabolic need during daytime. Instead, Osiecka et al. (2020) found that the clicking activity was best explained by light availability, as the acoustic activity increased with decreasing light availability. An increase in echolocation rate to compensate for the loss of visual information during dark hours have also previously been suggested as an explanation for the increased acoustic activity during nighttime (e.g. Carlström 2005). This hypothesis can however not explain the increase in FPP seen in this study, and together with the indications from our results that FPP was driving DPM h⁻¹, we argue that the increase in FPP during nighttime was caused by an actual increased foraging. All 6 survey sites displayed the same diel pattern, but clear spatial differences in levels of DPM h^{-1} and FPP was observed (Fig. 4).

Interestingly, there was a complete lack of FPP during daytime at Site 6, but rather high levels of FPP between 18:00 and 07:00 h (Fig. 4b). One possible

explanation for the nighttime foraging at all survey sites might be the presence of prey only being available, either by means of actual presence or behaviour, to the porpoises to predate on during nighttime, such as young cod Gadhus morhua, herring and sprat Sprattus sprattus. These fish species express diel vertical movement patterns in response to the diel vertical migration of their prey species (e.g. planktonic crustaceans and mysids; Cardinale et al. 2003, Axenrot et al. 2004, Espeland et al. 2010), resulting in a higher prey abundance in shallow waters and close to the surface during nighttime. Both cod and herring also reduce schooling and swimming speeds during nighttime due to relaxed predator avoidance mechanisms (Cardinale et al. 2003, Anderson et al. 2007, Didrikas & Hansson 2009), making them energetically beneficial to prey upon during nighttime by predators that do not rely on their vision for foraging, such as harbour porpoises. In addition, nighttime darkness could further benefit porpoises if their target prey is dependent on visual information to detect and avoid predation. Other potentially important prey species for harbour porpoises in the area include the sand goby Pomatoschistus minutus and other gobiid species (Andreasen et al. 2017). During the daytime in summer, the sand goby is buried in the muddy or sandy bottoms below the thermocline, i.e. below 10-15 m, but they actively swim and feed during the night (Ehrenberg & Ejdung 2008). During summer, predation on sand goby and other gobiids active at night may be one explanation for the higher DPM h⁻¹ and FPP observed during nighttime.

4.5. Lunar cyclicity

In addition to the diel cyclicity in DPM h^{-1} and FPP, the temporal analysis also revealed a periodic component corresponding to the lunar cycle at all 6 survey sites and in both variables (Table 3, Fig. 5). The lunar cyclicity was less distinct than the diel cyclicity and showed more variation, but the results still indicate an effect of the lunar cycle on harbour porpoise activity in the Kullen area. Lunar phase effects, from associated variations in potential lunar illumination or tidal forces, influence the distribution and behaviour of a wide range of marine species, from plankton to seals (e.g. Benoit-Bird et al. 2009a,b, Mercier et al. 2011, Fallows et al. 2016). For cetaceans, the lunar cycle affects the abundance of dusky dolphins Lagenorhynchus obscurus and spinner dolphins Stenella longirostris (Benoit-Bird et al. 2009b), the diving behaviour and habitat use of short-finned pilot whales *Globicephala macrorhynchus* (Owen et al. 2019), and foraging behaviour of common dolphins *Delphinus delphis* (Simonis et al. 2017).

In only a few studies have lunar phases been reported to impact harbour porpoise distribution (de Boer et al. 2014) and bycatch risk (Brennecke et al. 2021), while others have studied potential effects of the lunar cycle on harbour porpoise behaviour without finding any patterns (Osiecka et al. 2020). In addition, in regions where the lunar cycle creates strong tidal forces, these effects have been shown to influence harbour porpoise abundance and foraging behaviour (e.g. Pierpoint 2008, IJsseldijk et al. 2015, Holdman et al. 2019). However, to the best of our knowledge, the present study is the first to report lunar cycle effects on harbour porpoise foraging behaviour in an area without any notable tidal forcing. These results suggest that, apart from the indirect effects of the lunar cycle through tidal changes, harbour porpoises can be affected by the lunar cycle in other ways, such as through direct and indirect effects of varying light availability, which could influence predator-prey interactions and foraging efficiency. The indication of a somewhat higher porpoise presence and foraging activity during full moon for most survey sites (Fig. S2) may be explained by increased light availability, although we did not account for variation in cloud cover. Increased lunar illumination could make it easier for harbour porpoises to feed on prey species that normally use nighttime darkness as a predator avoidance technique, but with increasing light conditions would be more vulnerable to predation.

4.6. Implications for management

Harbour porpoises are vulnerable to human activities through bycatch in fishing nets (ICES 2019), adverse health effects caused by environmental pollutants (Siebert et al. 1999, Jepson et al. 2005, Murphy et al. 2015), disturbance of underwater noise from e.g. windfarm constructions and nearby boat passages (Dähne et al. 2013a, Wisniewska et al. 2018), and possibly also reduced access to high-quality prey (MacLeod et al. 2007). According to the EU Habitats Directive (Council Directive 92/43/EEC), Special Areas of Conservation (SACs) must be established for harbour porpoises, with the aim of maintaining or restoring the species at a favourable conservation status. By the end of 2021, the harbour porpoise was listed as a protected species in 253 SACs across European waters (European Environment Agency 2022). However, the designation of SACs does not protect the species in absence of appropriate management plans, and to do so multifaceted and adaptable conservation actions must be tailored to local conditions (Carlén et al. 2021, IAMMWG et al. 2015).

Our findings of micro-scale differences in detected porpoise presence and foraging activity provides insights for the development of effective protective measures for the species. For example, knowledge of micro-scale patterns in presence is crucial for optimal zonation of human activities within protected areas, which may both improve the efficiency of conservation actions and ease up challenges with conflicting interests. The high correlation between presence and foraging shows that presence is a good indicator of areas of energy intake and reveals how tightly linked the species is to its foraging areas. A tight link signals that these areas cannot easily be replaced by other areas, stressing the importance of low levels of disturbance and other pressures in these areas, and the need for an ecosystem approach in the management of local fish stocks. Further, the strong diel pattern indicates that there might also be a diel variation in bycatch risk, a factor that has achieved little attention so far (Northridge et al. 2017) and could be worth investigating further.

5. CONCLUSIONS

This study has revealed micro-scale variation in harbour porpoise Phocoena phocoena presence (DPM h⁻¹) and foraging activity (FPP) within a highly spatially restricted key area for the species, with striking differences between survey sites separated by only a few hundred meters. Harbour porpoise presence seems to be mainly driven by foraging opportunities, and the more frequently a site is used, the higher degree of foraging occurs. This is important information from a management point of view and for study design, as micro-scale spatial distribution needs to be considered in behavioural and conservation studies and actions. We conclude that time series analysis, including dynamic time warping and spectral analysis, seems to be a highly suitable method for analysis of acoustic time series data.

Acknowledgements. Many thanks to analyst Erland Lettevall PhD (Swedish Agency for Marine and Water Management) for important input and valuable discussions regarding management of the marine environment, species and habitats in relation to the ecology of marine mammals. We thank the Swedish Agency for Marine and Water Management for lending us the C-PODs used in this study. We thank the County Administrative Board of Skåne and Kullabergsguiderna AB, especially Daniel Åberg and David Arborelius, for assistance during deployment and retrieval of C-PODs. Field research was conducted under permit 521-6424-2014 from the County Adminstrative Board of Skåne. N.O. is financially supported by the Knut and Alice Wallenberg Foundation as part of the National Bioinformatics Infrastructure Sweden at SciLifeLab. We thank Erdem Özdes and Elise Palm for producing the map over the study area. We also thank the 3 reviewers for their comments and suggestions which greatly improved the manuscript.

LITERATURE CITED

- Aarefjord H, Bjørge AJ, Kinze CC, Lindstedt I (1995) Diet of the harbour porpoise (*Phocoena phocoena*) in Scandinavian waters. Rep Int Whaling Comm: Spec Issue 16: 211–222
- Alldredge AL, Hamner WM (1980) Recurring aggregations of zooplankton by a tidal current. Estuar Coast Mar Sci 10:31–37
- Amundin M, Carlström J, Thomas L, Carlén I, and others (2022) Estimating the abundance of the critically endangered Baltic proper harbour porpoise (*Phocoena phocoena*) population using passive acoustic monitoring. Ecol Evol 12:e8554
- Anderson JL, Laurel BJ, Brown JA (2007) Diel changes in behaviour and habitat use by age-0 Atlantic cod (Gadus morhua L.) in the laboratory and field. J Exp Mar Biol Ecol 351:267–275
- Andreasen H, Ross SD, Siebert U, Andersen NG, Ronnenberg K, Gilles A (2017) Diet composition and food consumption rate of harbor porpoises (*Phocoena phocoena*) in the western Baltic Sea. Mar Mamm Sci 33:1053–1079 Aphalo PJ (2015) The r4photobiology suite: spectral irradi
 - ance. UV4Plants Bull 2015(1):21–29
- Axenrot T, Didrikas T, Danielsson C, Hansson S (2004) Diel patterns in pelagic fish behaviour and distribution observed from a stationary, bottom-mounted, and upwardfacing transducer. ICES J Mar Sci 61:1100–1104
- Bagnall A, Lines J, Bostrom A, Large J, Keogh E (2017) The great time series classification bake off: a review and experimental evaluation of recent algorithmic advances. Data Min Knowl Discov 31:606–660
 - Barry JP, Dayton PK (1991) Physical heterogeneity and the organization of marine communities. In: Kolasa J, Pickett STA (eds) Ecological heterogeneity. Springer, New York, NY, p 270–320
- Benjamins S, van Geel N, Hastie G, Elliott J, Wilson B (2017) Harbour porpoise distribution can vary at small spatiotemporal scales in energetic habitats. Deep Sea Res II 141:191–202
- Benoit-Bird KJ, Au WWL, Wisdoma DW (2009a) Nocturnal light and lunar cycle effects on diel migration of micronekton. Limnol Oceanogr 54:1789–1800
- Benoit-Bird KJ, Dahood AD, Würsig B (2009b) Using active acoustics to compare lunar effects on predator-prey be-

Data availability. All processed data, R code files and workflow guidance to reproduce the time series analyses in this paper are available at Dryad, https://doi.org/10.5061/dryad. c59zw3rc0

havior in two marine mammal species. Mar Ecol Prog Ser 395:119–135

- Berndt DJ, Clifford AJ (1994) Using dynamic time warping to find patterns in time series. In: AAAIWS'94: Proc 3rd Int Conference on Knowledge Discovery and Data Mining. AAAI Press, Seattle, WA, p 359–370
- Booth CG, Embling C, Gordon J, Calderan SV, Hammond PS (2013) Habitat preferences and distribution of the harbour porpoise *Phocoena phocoena* west of Scotland. Mar Ecol Prog Ser 478:273–285
- Börjesson P, Berggren P, Ganning B (2003) Diet of harbor porpoises in the Kattegat and Skagerrak Seas: accounting for individual variation and sample size. Mar Mamm Sci 19:38–058
- Brandt MJ, Hansen S, Diederichs A, Nehls G (2014) Do man-made structures and water depth affect the diel rhythms in click recordings of harbor porpoises (*Phocoena phocoena*)? Mar Mamm Sci 30:1109–1121
- Brennecke D, Wahlberg M, Gilles A, Siebert U (2021) Age and lunar cycle predict harbor porpoise bycatch in the south-western Baltic Sea. PeerJ 9:e12284
- Carbone C, Gittleman JL (2002) A common rule for the scaling of carnivore density. Science 295:2273–2276
- Cardinale M, Casini M, Arrhenius F, Håkansson N (2003) Diel spatial distribution and feeding activity of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the Baltic Sea. Aquat Living Resour 16:283–292
- Carlén I, Thomas L, Carlström J, Amundin M, and others (2018) Basin-scale distribution of harbour porpoises in the Baltic Sea provides basis for effective conservation actions. Biol Conserv 226:42–53
- Carlén I, Nunny L, Simmonds MP (2021) Out of sight, out of mind: how conservation is failing European porpoises. Front Mar Sci :8:617478
- Carlström J (2005) Diel variation in echolocation behavior of wild harbor porpoises. Mar Mamm Sci 21:1–12
 - Chelonia Ltd (2014) CPOD.exe: a guide for users. https://www. chelonia.co.uk/cpod_downloads.htm (accessed 18 Jan 2022)
 - Chelonia Ltd (2015) C-POD user guide for C-PODs up to number 2089. https://www.chelonia.co.uk/cpod_ downloads.htm (accessed 18 Jan 2022)
- Clausen KT, Wahlberg M, Beedholm K, Deruiter S, Madsen PT (2011) Click communication in harbour porpoises Phocoena phocoena. Bioacoustics 20:1–28
- Dähne M, Gilles A, Lucke K, Peschko V, and others (2013a) Effects of pile-driving on harbour porpoises (*Phocoena phocoena*) at the first offshore wind farm in Germany. Environ Res Lett 8:025002
- Dähne M, Katharina Verfuss U, Brandecker A, Siebert U, Benke H (2013b) Methodology and results of calibration of tonal click detectors for small odontocetes (C-PODs). J Acoust Soc Am 134:2514–2522
- Davoren GK (2013) Distribution of marine predator hotspots explained by persistent areas of prey. Mar Biol 160: 3043-3058
- de Boer MN, Simmonds MP, Reijnders PJ, Aarts G (2014) The influence of topographic and dynamic cyclic variables on the distribution of small cetaceans in a shallow coastal system. PLOS ONE 9:e86331
- Didrikas T, Hansson S (2009) Effects of light intensity on activity and pelagic dispersion of fish: studies with a seabedmounted echosounder. ICES J Mar Sci 66:388–395
- Ehrenberg SZ, Ejdung G (2008) Daily activity pattern of the sand goby, *Pomatoschistus minutus* (Pisces), at low light intensity. Hydrobiologia 603:129–137

- Embling CB, Illian J, Armstrong E, van der Kooij J, Sharples J, Camphuysen KCJ, Scott BE (2012) Investigating finescale spatio-temporal predator-prey patterns in dynamic marine ecosystems: a functional data analysis approach. J Appl Ecol 49:481–492
- Espeland SH, Thoresen AG, Olsen EM, Stige LC, Knutsen H, Gjøsæter J, Stenseth NC (2010) Diel vertical migration patterns in juvenile cod from the Skagerrak coast. Mar Ecol Prog Ser 405:29–37
- European Environment Agency (2022) Natura 2000 network viewer. https://natura2000.eea.europa.eu/ (downloaded 27 Oct 2022)
- Fallows C, Fallows M, Hammerschlag N (2016) Effects of lunar phase on predator-prey interactions between white shark (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*). Environ Biol Fishes 99:805–812
- Fauchald P, Erikstad KE (2002) Scale-dependent predatorprey interactions: the aggregative response of seabirds to prey under variable prey abundance and patchiness. Mar Ecol Prog Ser 231:279–291
- Gallagher CA, Grimm V, Kyhn LA, Kinze CC, Nabe-Nielsen J (2021) Movement and seasonal energetics mediate vulnerability to disturbance in marine mammal populations. Am Nat 197:296–311
- Gilles A, Viquerat S, Becker EA, Forney KA, and others (2016) Seasonal habitat-based density models for a marine top predator, the harbor porpoise, in a dynamic environment. Ecosphere 7:e01367
- Giorgino T (2009) Computing and visualizing dynamic time warping alignments in R: the dtw package. J Stat Softw 31:1–24
- Holdman AK, Haxel JH, Klinck H, Torres LG (2019) Acoustic monitoring reveals the times and tides of harbor porpoise (*Phocoena phocoena*) distribution off central Oregon, USA. Mar Mamm Sci 35:164–186
 - IAMMWG, Camphuysen CJ, Siemensma ML (2015) A conservation literature review for the harbour porpoise (*Phocoena phocoena*). JNCC Rep No. 566, Peterborough
 - ICES (2019) Working Group on Marine Mammal Ecology (WGMME). ICES Sci Rep 1(22). http://doi.org/10.17895/ ices.pub.4980
- IJsseldijk LL, Camphuysen KCJ, Nauw JJ, Aarts G (2015) Going with the flow: tidal influence on the occurrence of the harbour porpoise (*Phocoena phocoena*) in the Marsdiep area. Neth J Sea Res 103:129–137
- Isojunno S, Matthiopoulos J, Evans PGH (2012) Harbour porpoise habitat preferences: robust spatio-temporal inferences from opportunistic data. Mar Ecol Prog Ser 448:155–170
- Jepson PD, Bennett PM, Deaville R, Allchin CR, Baker JR, Law RJ (2005) Relationships between polychlorinated biphenyls and health status in harbor porpoises (*Phocoena phocoena*) stranded in the United Kingdom. Environ Toxicol Chem 24:238–248
- Johnston DW, Westgate AJ, Read AJ (2005) Effects of finescale oceanographic features on the distribution and movements of harbour porpoises *Phocoena phocoena* in the Bay of Fundy. Mar Ecol Prog Ser 295:279–293
- Jones AR, Hosegood P, Wynn RB, De Boer MN, Butler-Cowdry S, Embling CB (2014) Fine-scale hydrodynamics influence the spatio-temporal distribution of harbour porpoises at a coastal hotspot. Prog Oceanogr 128:30–48
 - Kassambara A (2020) ggpubr: 'ggplot2' based publication ready plots. R package version 0.4.0. https://CRAN.Rproject.org/package=ggpubr

- Koblitz JC, Wahlberg M, Stilz P, Madsen PT, Beedholm K, Schnitzler HU (2012) Asymmetry and dynamics of a narrow sonar beam in an echolocating harbour porpoise. J Acoust Soc Am 131:2315–2324
- Koschinski S, Diederichs A, Amundin M (2008) Click train patterns of free-ranging harbour porpoises acquired using T-PODs may be useful as indicators of their behaviour. J Cetacean Res Manag 10:147–155
- Lawrence JM, Armstrong E, Gordon J, Lusseau SM, Fernandes PG (2016) Passive and active, predator and prey: using acoustics to study interactions between cetaceans and forage fish. ICES J Mar Sci 73:2075–2084
- MacLeod CD, Santos MB, Reid RJ, Scott BE, Pierce GJ (2007) Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: Could climate change mean more starving porpoises? Biol Lett 3:185–188
- Mercier A, Sun Z, Baillon S, Hamel JF (2011) Lunar rhythms in the deep sea: evidence from the reproductive periodicity of several marine invertebrates. J Biol Rhythms 26:82–86
- Miller LA, Wahlberg M (2013) Echolocation by the harbour porpoise: life in coastal waters. Front Physiol 4:52
- Moritz S, Bartz-Beielstein T (2017) imputeTS: time series missing value imputation in R. R J 9:207–218
- Murphy S, Barber JL, Learmonth JA, Read FL, and others (2015) Reproductive failure in UK harbour porpoises *Phocoena phocoena*: legacy of pollutant exposure? PLOS ONE 10:e0131085
- *Myers N (1988) Threatened biotas: 'hot spots' in tropical forests. Environmentalist 8:187–208
- Myrberg K, Andrejev O (2003) Main upwelling regions in the Baltic Sea—a statistical analysis based on threedimensional modelling. Boreal Environ Res 8:97–112
- Nielsen JR, Lundgren B, Jensen TF, Stæhr KJ (2001) Distribution, density and abundance of the western Baltic herring (*Clupea harengus*) in the Sound (ICES Subdivision 23) in relation to hydrographical features. Fish Res 50: 235–258
- Nielsen NH, Teilmann J, Sveegaard S, Hansen RG, Sinding MHS, Dietz R, Heide-Jørgensen MP (2018) Oceanic movements, site fidelity and deep diving in harbour porpoises from Greenland show limited similarities to animals from the North Sea. Mar Ecol Prog Ser 597:259–272
- Northridge S, Coram A, Kingston A, Crawford R (2017) Disentangling the causes of protected-species bycatch in gillnet fisheries. Conserv Biol 31:686–695
- Osiecka AN, Jones O, Wahlberg M (2020) The diel pattern in harbour porpoise clicking behaviour is not a response to prey activity. Sci Rep 10:14876
- Owen K, Andrews RD, Baird RW, Schorr GS, Webster DL (2019) Lunar cycles influence the diving behavior and habitat use of short-finned pilot whales around the main Hawaiian Islands. Mar Ecol Prog Ser 629:193–206
- Pierpoint C (2008) Harbour porpoise (Phocoena phocoena) foraging strategy at a high energy, near-shore site in south-west Wales, UK. J Mar Biol Assoc UK 88:1167–1173
- Pirotta E, Thompson PM, Miller PI, Brookes KL, and others (2014) Scale-dependent foraging ecology of a marine top predator modelled using passive acoustic data. Funct Ecol 28:206–217
 - R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
 - Read AJ (1999) Harbour porpoise—*Phocoena phocoena* (Linneaus 1758). In: Ridway SH, Harrison SR (eds) Hand-

book of marine mammals. The second book of dolphins and porpoises, Vol 6. Academic Press, San Diego, CA, p323-356

- Rojano-Doñate L, McDonald BI, Wisniewska DM, Johnson M, and others (2018) High field metabolic rates of wild harbour porpoises. J Exp Biol 221:jeb185827
- Russell RW, Hunt GL, Coyle KO, Cooney RT (1992) Foraging in a fractal environment: spatial patterns in a marine predator-prey system. Landsc Ecol 7:195–209
 - Santos MB, Pierce GJ (2003) The diet of harbour porpoise (*Phocoena phocoena*) in the northeast Atlantic. Oceanogr Mar Biol Annu Rev 41:355–390
- Schaffeld T, Bräger S, Gallus A, Dähne M and others (2016) Diel and seasonal patterns in acoustic presence and foraging behaviour of free-ranging harbour porpoises. Mar Ecol Prog Ser 547:257–272
- Siebert U, Joiris C, Holsbeek L, Benke H, Failing K, Frese K, Petzinger E (1999) Potential relation between mercury concentrations and necropsy findings in cetaceans from German waters of the North and Baltic Seas. Mar Pollut Bull 38:285–295
- Simon M, Nuuttila H, Reyes-Zamudio MM, Ugarte F, Verfub U, Evans PGH (2010) Passive acoustic monitoring of bottlenose dolphin and harbour porpoise, in Cardigan Bay, Wales, with implications for habitat use and partitioning. J Mar Biol Assoc UK 90:1539–1545
- Simonis AE, Roch MA, Bailey B, Barlow J and others (2017) Lunar cycles affect common dolphin *Delphinus delphis* foraging in the Southern California Bight. Mar Ecol Prog Ser 577:221–235
- Skov H, Thomsen F (2008) Resolving fine-scale spatio-temporal dynamics in the harbour porpoise *Phocoena phocoena*. Mar Ecol Prog Ser 373:173–186
 - SMHI (2014) Tides. www.smhi.se/en/theme/tides-1.11272 (accessed 14 Apr 2022)
 - SMHI (2021) Surface currents. www.smhi.se/en/theme/ surface-currents-1.12286 (accessed 14 Apr 2022)
- Sørensen PM, Wisniewska DM, Jensen FH, Johnson M, Teilmann J, Madsen PT (2018) Click communication in wild harbour porpoises (*Phocoena phocoena*). Sci Rep 8:9702
- Spitz J, Trites AW, Becquet V, Brind'Amour A, Cherel Y, Galois R, Ridoux V (2012) Cost of living dictates what whales, dolphins and porpoises eat: the importance of prey quality on predator foraging strategies. PLOS ONE 7:e50096
- Stephens DW, Krebs JR (1986) Foraging theory, Vol 1. Princeton University Press, Princeton, NJ
- Stephens DW, Brown JS, Ydenberg RC (2007) Foraging: behavior and ecology. University of Chicago Press, Chicago, IL
 - Stevick P, McConnell B, Hammond P (2002) Patterns of movement. In: Hoelzel R (ed) Marine mammal biology: an evolutionary approach. Blackwell, Oxford, p 185–216
- Sveegaard S, Teilmann J, Berggren P, Mouritsen KN, Gillespie D, Tougaard J (2011a) Acoustic surveys confirm the high-density areas of harbour porpoises found by satellite tracking. ICES J Mar Sci 68:929–936
- Sveegaard S, Teilmann J, Tougaard J, Dietz R, Mouritsen KN, Desportes G, Siebert U (2011b) High-density areas for harbor porpoises (*Phocoena phocoena*) identified by satellite tracking. Mar Mamm Sci 27:230–246
- Sveegaard S, Andreasen H, Mouritsen KN, Jeppesen JP, Teilmann J, Kinze CC (2012a) Correlation between the seasonal distribution of harbour porpoises and their prey in the Sound, Baltic Sea. Mar Biol 159:1029–1037

- Sveegaard S, Nabe-Nielsen J, Stæhr KJ, Jensen TF, Mouritsen KN, Teilmann J (2012b) Spatial interactions between marine predators and their prey: herring abundance as a driver for the distributions of mackerel and harbour porpoise. Mar Ecol Prog Ser 468:245–253
- Swartzman G (1994) Relating the distribution of pollock schools in the Bering Sea to environmental factors. ICES J Mar Sci 51:481–492
 - Teilmann J, Sveegaard S, Dietz R, Petersen IK, Berggren P, Desportes G (2008) High density areas for harbour porpoises in Danish waters. NERI Technical Report No 657, National Environemental Research Institute, University of Aarhus
 - Teilmann J, Dietz R, Sveegaard S (2022) The use of marine waters in Skåne by harbour porpoises in time and space. Tech Rep No. 236. DCE – Danish Centre for Environment and Energy, Aarhus University. http://dce2.au.dk/ pub/TR236.pdf
- *Thompson SA, Sydeman WJ, Santora JA, Black BA, and others (2012) Linking predators to seasonality of upwelling: using food web indicators and path analysis to infer trophic connections. Prog Oceanogr 101: 106–120
- Todd VLG, Pearse WD, Tregenza NC, Lepper PA, Todd IB (2009) Diel echolocation activity of harbour porpoises (*Phocoena phocoena*) around North Sea offshore gas installations. ICES J Mar Sci 66:734–745
- Verfuß UK, Miller LA, Schnitzler HU (2005) Spatial orientation in echolocating harbour porpoises (*Phocoena phocoena*). J Exp Biol 208:3385–3394
- Verfuß UK, Miller LA, Pilz PK, Schnitzler HU (2009) Echolocation by two foraging harbour porpoises (*Phocoena phocoena*). J Exp Biol 212:823–834
- Verfuß UK, Dahne M, Gallus A, Jabbusch M, Benke H (2013) Determining the detection thresholds for harbor porpoise clicks of autonomous data loggers, the

Editorial responsibility: Lisa Ballance, Newport, Oregon, USA

Reviewed by: B. Wilson, J. Gordon and 1 anonymous referee

timing porpoise detectors. J Acoust Soc Am 134: 2462-2468

- Villadsgaard A, Wahlberg M, Tougaard J (2007) Echolocation signals of wild harbour porpoises, *Phocoena phocoena*. J Exp Biol 210:56–64
 - Wändahl T (1980) Hydrografi. In: Öresund. Tillstånd effekter av närsalter. Öresundskommissionen. Liber, Stockholm
- Williamson LD, Brookes KL, Scott BE, Graham IM, and others (2016) Echolocation detections and digital video surveys provide reliable estimates of the relative density of harbour porpoises. Methods Ecol Evol 7:762–769
- Williamson LD, Scott BE, Laxton MR, Bachl FE, Illian JB, Brookes KL, Thompson PM (2022) Spatiotemporal variation in harbor porpoise distribution and foraging across a landscape of fear. Mar Mamm Sci 38:42–57
- Wisniewska DM, Johnson M, Teilmann J, Rojano-Donate L, and others (2016) Ultra-high foraging rates of harbor porpoises make them vulnerable to anthropogenic disturbance. Curr Biol 26:1441–1446
- Wisniewska DM, Johnson M, Teilmann J, Siebert U, Galatius A, Dietz R, Madsen PT (2018) High rates of vessel noise disrupt foraging in wild harbour porpoises (*Phocoena phocoena*). Proc Biol Sci 285:20172314
- Wolanski E, Hamner WM (1988) Topographically controlled fronts in the ocean and their biological influence. Science 241:177–181
- Womble JN, Sigler MF (2006) Seasonal availability of abundant, energy-rich prey influences the abundance and diet of a marine predator, the Steller sea lion *Eumetopias jubatus*. Mar Ecol Prog Ser 325:281–293
- Yu G (2020) Using ggtree to visualize data on tree-like structures. Curr Protoc Bioinformatics 69:e96
- Zein B, Woelfing B, Dahne M, Schaffeld T, and others (2019) Time and tide: seasonal, diel and tidal rhythms in Wadden Sea harbour porpoises (*Phocoena phocoena*). PLOS ONE 14:e0213348

Submitted: June 15, 2022 Accepted: February 15, 2023 Proofs received from author(s): March 7, 2023