Agenda Item 11 | Funding of Projects Supported by ASCOBANS

Progress of Projects Supported by ASCOBANS

BALHAB

Document Inf.11.1.a | **Project Report to ASCOBANS for the Project "Baltic Sea Harbour Porpoise Foraging Habitats BALHAB"**

Action Requested

- Take note

Submitted by

Aarhus University
Coalition Clean Baltic (CCB)
Swedish Museum of Natural History

NOTE:
DELEGATES ARE KINDLY REMINDED
TO BRING THEIR OWN COPIES OF DOCUMENTS TO THE MEETING

Secretariat's Note

The Rules of Procedure adopted at the ASCOBANS 8th Meeting of Parties remain in force until and unless an amendment is called for and adopted.

BALHAB

Project report to ASCOBANS for the project "Baltic Sea Harbour porpoise foraging habitats (BALHAB)"

Scientific Report from DCE – Danish Centre for Environment and Energy No. 287 2018

AARHUS UNIVERSITY
DCE – DANISH CENTRE FOR ENVIRONMENT AND ENERGY

[Blank page]

BALHAB

Project report to ASCOBANS for the project "Baltic Sea Harbour porpoise foraging habitats (BALHAB)"

Scientific Report from DCE – Danish Centre for Environment and Energy No. 287 2018

Line A. Kyhn[1]
Ida Carlén[2]
Julia Carlström[3]
Jakob Tougaard[1]

[1] Aarhus University, Department of Bioscience
[2] Coalition Clean Baltic
[3] Swedish Museum of Natural History

AARHUS UNIVERSITY
DCE – DANISH CENTRE FOR ENVIRONMENT AND ENERGY

Data sheet

Series title and no.: Scientific Report from DCE – Danish Centre for Environment and Energy No. 287

Title: BALHAB
Subtitle: Project report to ASCOBANS for the project "Baltic Sea Harbour porpoise foraging habitats (BALHAB)"

Authors: Line A. Kyhn[1], Ida Carlén[2], Julia Carlström[3] and Jakob Tougaard[1]

Institutions: [1])Aarhus University, Department of Bioscience
[2])Coalition Clean Baltic
[3])Swedish Museum of Natural History

Publisher: Aarhus University, DCE – Danish Centre for Environment and Energy ©
URL: http://dce.au.dk/en

Year of publication: August 2018
Editing completed: August 2018

Referee: Signe Sveegaard
Quality assurance, DCE: Kirsten Bang

Financial support: ASCOBANS

Please cite as: Kyhn, L.A., Carlén, I., Carlström, J. and Tougaard, J. 2018. BALHAB. Project report to ASCOBANS for the project "Baltic Sea Harbour porpoise foraging habitats (BALHAB)". Aarhus University, DCE – Danish Centre for Environment and Energy, 24 pp. Scientific Report No. 287. http://dce2.au.dk/pub/SR287.pdf

Abstract: The harbour porpoise is protected by the Habitats Directive Annexes II and IV. This means that a system of strict protection shall be established throughout its natural range (Annex IV), and that sites of significant importance to the species should be designated and protected (special areas of conservation) (Annex II). Preferred foraging habitats could be considered candidates for special areas of conservation. Here we investigated whether foraging areas can be identified in the acoustic data from the SAMBAH project. Feeding buzzes were extracted from the SAMBAH dataset. Feeding buzz ratio was higher in the Baltic Proper than in the SW Baltic. In the entire SAMBAH study area, the feeding buzz ratio was significantly higher during dawn and night. Specific foraging areas within the high-density areas was not found, supporting the theory that porpoises have to feed almost constantly and that porpoises occur where they can feed.

Keywords: Passive acoustic monitoring, foraging, SAC, Habitats Directive

Layout: Graphic Group
Front page photo: Olli Loisa

ISBN: 978-87-7156-353-5
ISSN (electronic): 2245-0203

Number of pages: 24

Internet version: The report is available in electronic format (pdf) at http://dce2.au.dk/pub/SR287.pdf

Contents

[Blank page]

Summary

The harbour porpoise (*Phocoena phocoena*) is the most common cetacean in northern Europe, however, the Baltic Proper sub-population is listed as critically endangered by IUCN (Hammond et al. 2008). The harbour porpoise is protected by the Habitats Directive Annexes II and IV. This means that a system of strict protection (Habitat Directive Article 12) shall be established throughout its natural range (Annex IV), and that sites of significant importance to the species should be designated and protected (Annex II). Preferred foraging habitats may be considered as candidates for special areas of conservation in accordance with the requirements of the Habitat Directive (Annex II). The main purpose of this project was to investigate whether foraging areas for harbour porpoises can be identified by comparing the occurrence of foraging events, i.e. echolocation buzzes, in relation to harbour porpoise presence in the acoustic data from the SAMBAH project – a five-year study with 304 passive acoustic dataloggers deployed for two consecutive years (www.sambah.org). The acoustic data were analysed in accordance with the posed hypothesize; that the proportion of buzzes would vary between stations and in time, indicating that some areas and times of the day / times of the year are more important than others, in terms of foraging.

Extraction of feeding buzzes was automated from the large SAMBAH dataset and based hereon we show that the feeding ratio for harbour porpoises is higher in the Baltic Proper than in the SW Baltic, and that in the entire SAMBAH study area, the feeding buzz ratio is significantly higher during dawn and night than during the day and dusk. We could not identify foraging areas within the high-density areas for harbour porpoises, which supports the theory that porpoises have to feed almost constantly and hence that porpoises occur where they can feed.

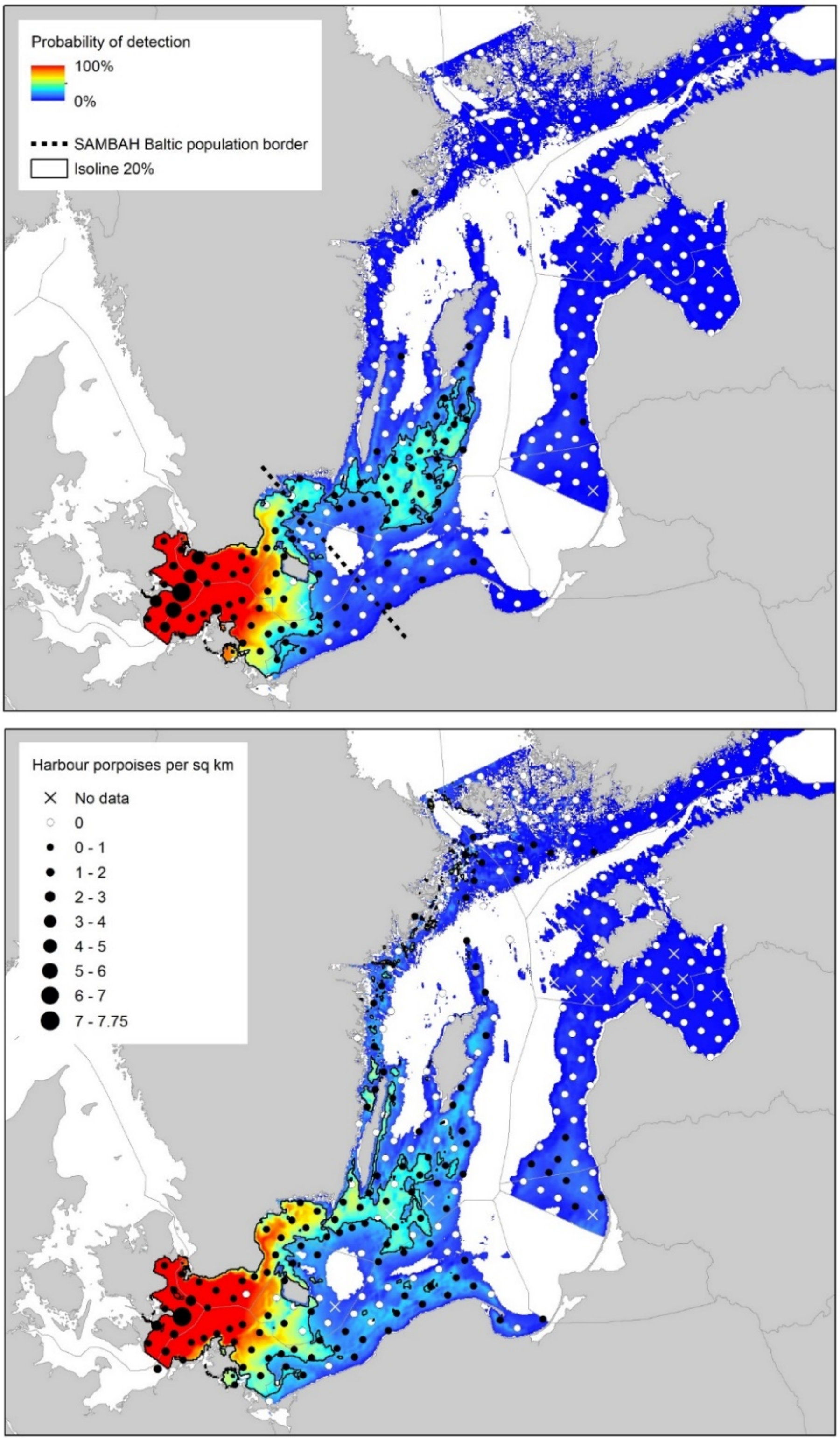
Altogether, the results underline that harbour porpoises rightly are placed on the Habitat Directive's Annex IV, implying that the animals should be protected throughout their distribution range. This may seem to be in conflict with the requirements of Annex II to designate areas of special importance for the species. However, the indications that lead to the conclusion that porpoises are feeding almost continuously must then mean that the most important areas for foraging are also the areas where the densities are highest. It also means that, in order to increase the chances for a positive development of the critically endangered Baltic Proper harbour porpoise population, management plans with actual conservation measures should be implemented in the designated Natura 2000 sites.

1. Introduction

The harbour porpoise (*Phocoena phocoena*) is the most common cetacean in northern Europe, however, the Baltic Proper sub-population is listed as critically endangered by IUCN (Hammond et al. 2008). The harbour porpoise is protected by the Habitats Directive Annexes II and IV. This means that a system of strict protection (Habitat Directive Article 12) shall be established throughout its natural range (Annex IV), and that sites of significant importance to the species should be designated and protected (Annex II). For animal species ranging over wide areas, such as harbour porpoises, those sites should present physical or biological factors essential to their life and reproduction. However, it is challenging to identify such areas for wide-ranging and elusive species such as harbour porpoises. Studies on physiology and energetics suggests that small cetaceans have a higher metabolic rate than similarly sized terrestrial mammals, likely due to the higher heat loss to the water (Williams and Maresh, 2016). This means a constant and high demand for energy intake. For porpoises, this presumption is supported by recent measurements from acoustic tags deployed on wild porpoises. These recordings showed that the tagged porpoises fed almost continuously (Wisniewska et al., 2016) for the duration of the measurements (up to 23 hours) with a foraging rate of up to 550 small fish per hour and an estimated >90% success rate. Feeding events, both successful and attempts, were identified by the highly stereotypical echolocation sequence leading up to an approach to prey, known as a feeding buzz (Miller et al., 1995; Verfuß et al., 2009). This feeding buzz is characterized by a very rapid click repetition rate and this feature has previously been used to identify putative foraging activity in passive acoustic recordings of porpoise clicks (Carlstrøm, 2005; Todd et al., 2009). High repetition rate clicks as a proxy for feeding buzzes may therefore be a good candidate as an indicator for preferred foraging habitats, which in turn can be considered as candidates for special areas of conservation in accordance with the requirements of the Habitat Directive (Annex II). All relevant EU member states already have Natura 2000 sites with harbour porpoises listed as occurring species. Data on preferred foraging habitats herein could be used to manage and regulate anthropogenic activities inside the Natura 2000 areas to adequately protect harbour porpoises.

Acoustic recordings from a foraging area are therefore expected to contain a high proportion of high repetition rate clicks in relation to low-repetition rate clicks (Pirotta et al. 2014). Other studies have found that occurrence of buzzes varies temporally and spatially (Benjamins et al., 2017; Carlstrøm, 2005; Todd et al., 2009), which is a good indication that buzzes can be used to signify important foraging habitats for harbour porpoises. The main purpose of this project was to investigate whether foraging areas for harbour porpoises could be identified by comparing the occurrence of foraging events, i.e. buzzes, in relation to harbour porpoise presence in the acoustic data from the SAMBAH project (www.SAMBAH.org). Further, we investigated whether the proportion of buzzes varied among the four diel phases dawn, day, dusk and night. We hypothesize that the proportion of buzzes varies between stations and in time, indicating that some areas and times of the day / times of the year are more important than others, in terms of foraging.

Figure 1.1. Distribution maps of harbour porpoises (probability of detection and density) within the SAMBAH study area produced by spatial modelling. The top map show the average from May to October and the lower map November to April.



The SAMBAH dataset was collected by deploying acoustic dataloggers (CPODs) in a regular grid consisting of 304 stations across the study area in the Baltic. Two years of data was collected, from May 2011 to April 2013, comprising a very large dataset for examining whether buzzes may be used to designate foraging habitats.

The SAMBAH data has already been used to identify important areas (ASCOBANS, 2016; Carlström and Carlen, 2016) for harbour porpoises and special areas of conservation has been appointed in Swedish Waters on this background. Together with the SAMBAH results on detection rate, density and abundance (**Figure 1.1**) the output from BALHAB may serve as a thorough basis for designation and evaluation of protected areas and development and implementation of a strict system of protection throughout the distribution range of harbour porpoises in the Baltic Sea.

2. Materials and methods

2.1 Passive acoustic monitoring (PAM)

The data used in this study was collected during the SAMBAH project that ran from 2010-2015. During a total of 2 years (May 2011 - April 2013), harbour porpoise click detectors, so called CPODs (Chelonia Ltd., UK), were deployed at 304 stations in a systematic grid with 23.5 kilometers between individual stations, all in areas with a water depth between 5 and 80 m. (**Figure 2.1**). CPODs are self-contained dataloggers designed to detect and store harbour porpoises' echolocation clicks (**Figure 2.1**). It runs on ten D-cell batteries and can record for up to six months at a time. Data is stored on an SD-memory card. All settings were pre-set in each unit by the manufacturer and all units were individually calibrated to ensure comparable performance. The datalogger stores information about individual clicks, such as time, duration, mean instantaneous frequency and peak amplitude.

Passive acoustic monitoring of porpoises is efficient because they, as other toothed whales, echolocate. The echolocation sounds of harbour porpoise are well described and highly stereotypical and unlike most other natural sounds in the Baltic Sea. They emit stereotypic high-frequency clicks with a centre frequency of around 130 kHz (Kyhn et al., 2013; Villadsgaard et al., 2007). The click is of narrow bandwidth and contains essentially no energy below 100 kHz. No other known organisms in the Baltic Proper emits similar sounds (although some enigmatic sounds, referred to as weak ultrasonic transients, or WUTs, remain unidentified, see Tregenza, 2013). Boat sonars can be of similar frequency but has a constant click repetition rate making them easy to distinguish from porpoises click trains. For reliable identification of harbour porpoise click trains, the CPOD data was first filtered and the sound sources classified using the proprietary KERNO algorithm. Secondly, the extracted click trains were filtered with the Baltic Sea specific Hel1-extension in the associated CPOD.exe software.

Each CPOD was placed with the hydrophone 2 m above the seafloor. The SAMBAH project was defined to be within waters between 5 and 80 m depth, partially due to logistic constraints, and partially due to permanent hypoxic conditions (<2ml O2/l) in deeper areas (Carstensen et al., 2014; Hansson and Andersson, 2016), making these unsuitable habitat for bottom dwelling fish and are thereby expected to host low porpoise densities. These areas are indicated as white on the map and together with the Bothnian Bay, these were excluded because the porpoise densities was expected to be negligible in this area, and the Russian EEZs, which could not be part of the EU funded project (**Figure 2.1**).

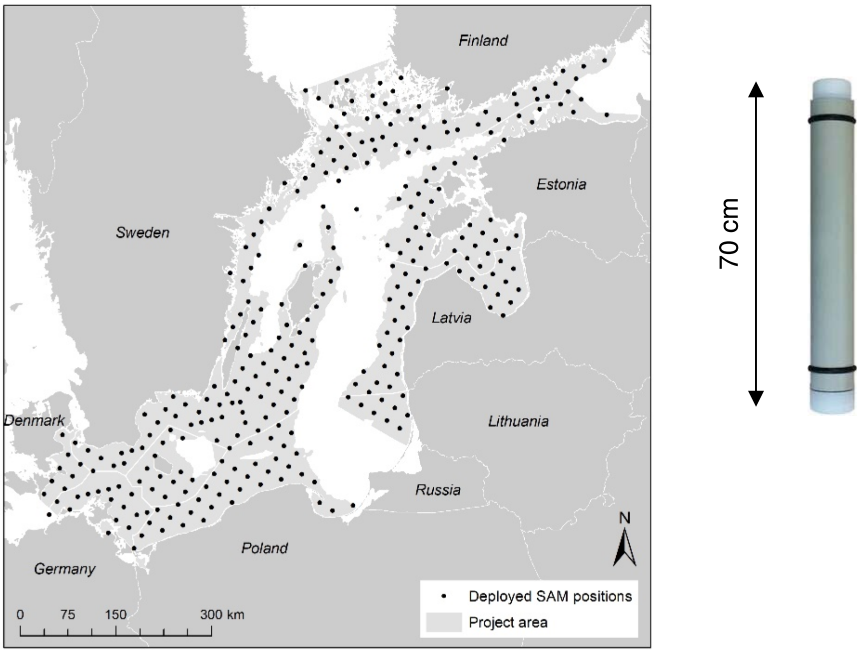


Figure 2.1. Map showing the positions of the 304 passive acoustic dataloggers (CPODs) deployed to detect harbour porpoises during the SAMBAH project from 2011 to 2013. The white areas in the map signify water depths above 80 m excluded in the SAMBAH project. To the right is a CPOD. The hydrophone is mounted inside the white cap at the top

2.1.1 Acoustic data analysis

The Hel1 algorithm (Hel1) was specifically developed to find click trains in the SAMBAH data, aiming to ensure a very low level of false positives in the Baltic environment. False positives are particularly problematic in low density areas. The Baltic Proper has an extremely low density of harbour porpoises and the possible bias from false positives is potentially much larger than in high density areas, such as the Inner Danish Waters, where false detections only constitute a small proportion of all detections. Thus, the lower the probability of true positives, the more conservative a classifier should be used. For that reason the data used in this study were filtered with the very conservative Hel 1 algorithm. In addition to the automatic filtering, all files with an average detection rate of less than 60 detection-positive minutes per year were visually inspected by a team of trained people. Click trains identified as not originating from harbour porpoises were marked and excluded from further analyses.

2.1.2 Detection of foraging events

The SAMBAH project showed that some areas within the Baltic Sea were more important for harbour porpoises than others (**Figure 1.1**). The main purpose of the BALHAB study was to determine whether, within these important areas, sub-areas more important for foraging than others could be identified. Also the temporal aspect was taken into consideration.

For this purpose, we adapted the methodology of Pirotta et al. (2014). Time stamps of all individual clicks classified as porpoises by the HEL1 classifier were exported as text files by the CPOD.exe software and imported into a custom written Matlab script (Mathworks Inc., R2014b). Based on the procedure adopted by (Pirotta et al., 2014), click intervals within click trains identified by CPOD.exe were classified as either high-repetition rate (indicative of a buzz) or low-repetition rate (indicative of search phase clicks). Pirotta et al., (2014) used an adaptive modelling procedure to determine the best cut-off value between the two classes. We found that this procedure did not work for the SAMBAH data due to the overall much lower number of clicks and instead we adopted a fixed criterion of 15 ms based on Wisniewska et al. (2012). Inter-train intervals were excluded from analysis.

Inter-click-intervals (ICIs) were extracted minute by minute and for each station and Julian day grouped into diel phases. Sunrise, sunset and twilight was computed for each Julian day for each station by means of the Matlab function sunset (courtesy M. Mahooty, Mathlab file exchange) and used to define the diel phases for each station and each Julian day as (**Table 2.1**.):

Table 2.1. Definitions of diel phases.

Phase	Start	End
Dawn	Sunrise - duration of civil twilight	Sunrise + duration of civil twilight
Day	Sunrise + duration of civil twilight	Sunset - duration of civil twilight
Dusk	Sunset - duration of civil twilight	Sunset + duration of civil twilight
Night	Sunset + duration of civil twilight	Sunrise following day - duration of civil twilight

The buzz ratio (BR) was calculated for each station, day and diel phase as

$$BR = \frac{N_{high}}{N_{high} + N_{low}} \cdot 100\%$$

where N_{high} is the number of click intervals less than 15 ms within the given period and N_{low} is the number of click intervals 15 ms or more within the given period.

2.2 Spatial and temporal modelling

The proportion of feeding buzz inter-click intervals per station, day and diel phase were used to investigate the spatial and temporal distribution of feeding events in the study area. Thereby one station can have a maximum of four data points for one day; one for each diel phase. Only records that had nine or more porpoise positive minutes (PPM) in a diel phase per day were used in these analyses, where one porpoise positive minute indicates that porpoise clicks were detected within that particular minute. This meant that, after removing three spatial outliers in the eastern and northern SAMBAH study area, data was spatially restricted to two clusters: one in the southwest Baltic (referred to as SW Baltic in the following) and one around Hoburg's Bank and the Northern and Southern Mid-sea Banks in the Baltic Proper (referred to as Baltic Proper in the following) (Shown in the Results section in **Figure 3.1**.).

Models of proportion of feeding buzzes based on spatial and temporal predictor variables were fit with 'Random Forest for R' (version 4.6-12) in R version 3.4.1 (R Core Team, 2017). Random Forest utilizes a machine-learning algorithm to fit small classification or regression tree models to produce a combined result (i.e. the forest) for prediction (Breiman, 2001). The method can be used for very large datasets, and it automatically fits complex interactions between predictor variables and estimates predictor variable importance (Cutler et al., 2007).

The explanatory variables depth, aspect, and the topographic complexity index (TCO) were based on the Baltic Sea Bathymetry Database (HELCOM, 2015) with 500 m resolution. The topographic position index (TPI) was based on the same bathymetric dataset but set to represent a larger scale (see explanation **Table 2.2**). Diel phase was included in the models, and time of year was taken into account in all models by including month. Correlograms were inspected to ensure that correlated covariates were not used in the same model, and a variance inflation factor (G-VIF) threshold was set to 3, as suggested by Zuur et al. (2010), to avoid problems due to multi-collinearity. Neither was a problem and all predictor variables could be included in all models.

Differences in feeding buzz ratios between spatial clusters and diel phases were tested using the Kruskal-Wallis non-parametric rank sum test (Hollander et al., 2013) in the native statistics package in R version 3.4.1 (R Core Team, 2017), and pairwise Wilcoxon Rank tests with Benjamini & Hochberg (Benjamini and Hochberg, 1995) adjustment of *p*-values for multiple comparisons.

It should be noted that we did not attempt to control for spatio-temporal variation in detectability due to factors such as variation in depth, temperature, salinity and animal behaviour (see Discussion).

Table 2.2. Covariates available for modelling.

Covariate	Abbreviation	Value ranges	Explanation
Depth	Depth	5 – 80	Average depth in meters within a radius of 2.5 km.
Aspect	Aspect	0 – 360	Average direction of the slope, in degrees from north within a radius of 2.5 km.
Topographic complexity index	TCO	9.719e-05 - 5.340e-02	Topographic complexity index calculated by multiplying scaled values for slope and aspect (Bouchet et al., 2015; Carroll et al., 2001) averaged within a radius of 2.5 km. Describes the degree of complexity of the sea floor.
Topographic position index	TPI	-33 – 81	Topographic position index calculated as the difference between the elevation of the cell and the mean elevation for all cells in a moving annulus (Bouchet et al., 2015; Dickson and Beier, 2007) with an inner radius of 25 km and an outer radius of 50 km. Describes if the area is on average higher or lower than surrounding areas.
Bottom salinity	Btmsalmn	6.8 – 10.1 psu	Monthly mean of bottom salinity from oceanographic model
Surface salinity	Sfcsalmn	6.6 – 9.4 psu	Monthly mean of surface salinity from oceanographic model
Bottom temperature	Btmtemmn	1.7 – 18.8 °C	Monthly mean of bottom temperature from oceanographic model
Surface temperature	Sfctemmn	1.5 – 19.0 °C	Monthly mean of surface temperature from oceanographic model
Bottom speed	Btmspdmn	0 – 5.1 m/s	Monthly mean of bottom current speed from oceanographic model
Surface speed	Sfcspdmn	0 – 10.6 m/s	Monthly mean of surface current speed from oceanographic model
Pycnocline gradient	pclgramn	-0.44 – 0.11	Monthly mean of the strength of the pycnocline gradient from oceanographic model
Month	Month	1 – 12	Calendar month, 1-12, used with a circular smooth.
Diel phase	Diel_phase	1 – 4	Factor variable. Dawn (1), day (2), dusk (3) and night (4)
Geographical coordinates	UTMX, UTMY	UTMX 695965 – 1517390 UTMY 5990084 – 6828455	Geographical coordinates in UTM32N. Always used as a 2D smooth by Month.

3. Results

The analysis focused on finding important foraging habitats for porpoises in the Baltic. A graphical display of all stations where nine or more porpoise positive minutes per day and diel phase were detected reveals two spatial clusters within the dataset (**Figure 3.1**): the SW Baltic west of Bornholm, and the Baltic Proper around the offshore banks south of Öland and Gotland. The separation between the two is consistent with the previous SAMBAH study (Carlén et al., 2018), based on the same data set. Number of data points per diel phase and total data points are shown in **Table 3.1**. From **Table 3.1** it is obvious that the detection rate is much lower in the Baltic Proper than in the SW Baltic.

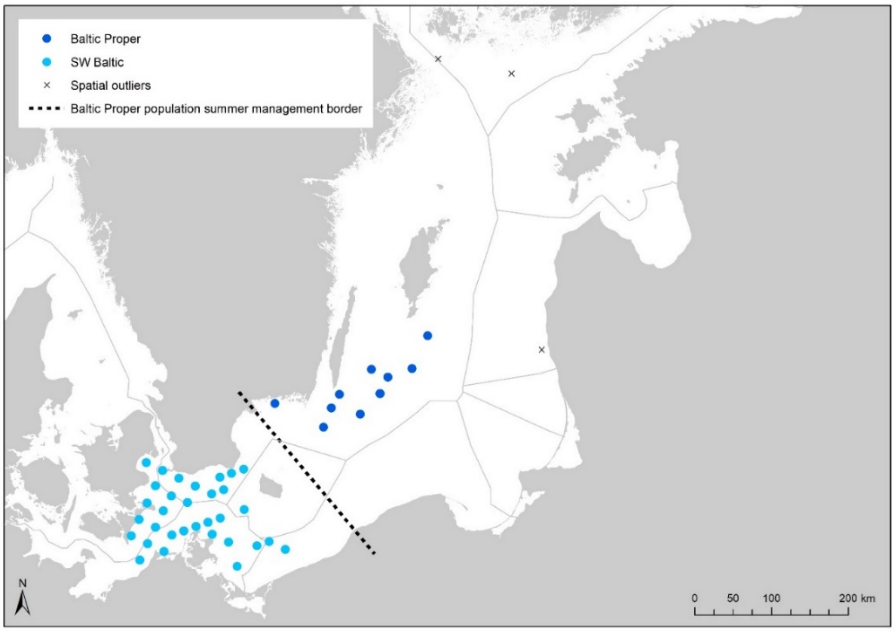


Figure 3.1. SAMBAH monitoring stations included in the BALHAB data set based on the criterion of ≥9PPM per day and diel phase. Spatial outliers, which fulfilled the criterion for inclusion, but were deemed uninformative with respect to the model and hence removed, are marked with x. The closest of the excluded stations (Latvian coast) was 149 km from the closest station included.

Table 3.1. Data points per subarea and diel phase. All stations with ≥9porpoise positive minutes per diel phase were included in the analysis.

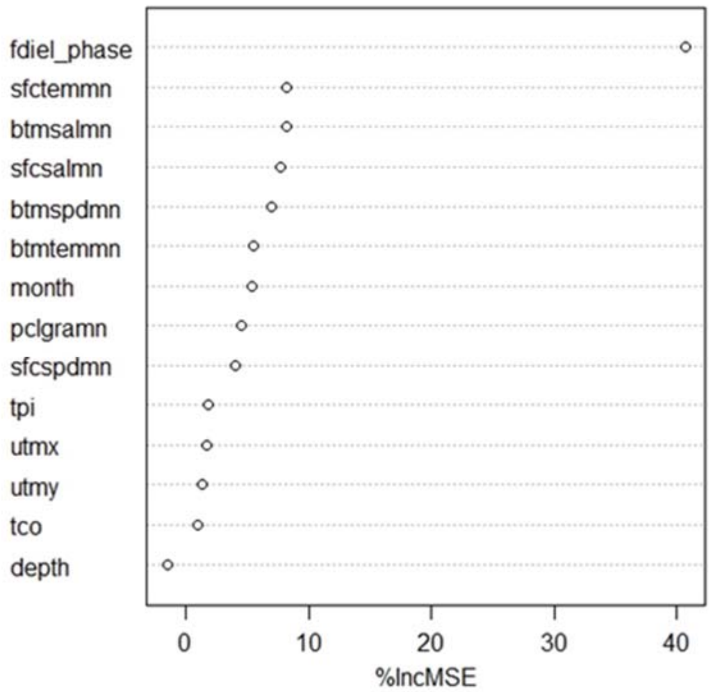
	Dawn	Day	Dusk	Night	Total
SW Baltic	233	1341	200	1712	3486
Baltic Proper	7	73	5	39	124
Total	240	1414	205	1751	3610

3.1 Spatial and temporal analyses

3.1.1 Spatial analyses

The first model using data points from both areas and all explanatory variables explained 21.7% of the variance, with diel phase being the most important explanatory variable. When removing diel phase, the model explained 18.2% of the variation, with some of the oceanographic variables, depth and month explaining most of the variation. The model using only data from the Baltic Proper and including diel phase, explained 39.7% of the variation, with diel phase as the primary explanatory variable (**Figure 3.2**). When diel phase was removed, the model explained 10.1% of the variation.

Figure 3.2. Importance of predictor variables in random forest model using data from the Baltic Proper, shown as increase in Mean Squared Error of predictions as a result of the variable being permuted.

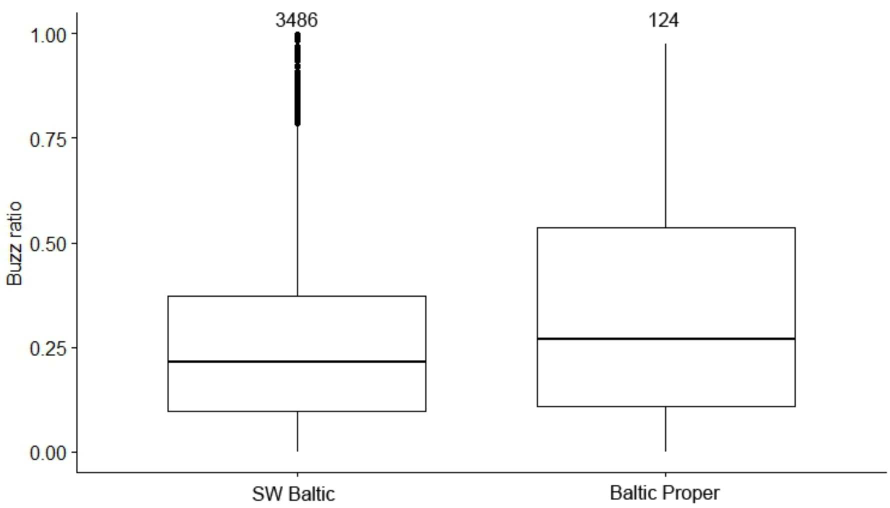


The overall buzz ratio of the total dataset (SW Baltic and Baltic Proper) was 26.2%. The overall buzz ratio of the two sub areas, Baltic Proper and SW Baltic, was statistically compared and proved significantly different (Kruskal-Wallis chi-squared = 8.9363, df = 1, *p*-value = 0.0028) with a higher mean buzz ratio in the Baltic Proper (average of 35.3 % as opposed to 26.0 % in the SW Baltic (**Figure 3.2** and **Figure 3.3**).

Table 3.2. Percentage of high-repetition rate click intervals in relation to low-repetition rate click intervals in the four diel phases calculated for the entire area, per sub area and total.

	Dawn	Day	Dusk	Night	Total
SW Baltic	34.2%	22.7%	23.0%	27.7	26.0%
Baltic Proper	51.9%	20.8%	19.3%	61.6%	35.3%
Total	34.7%	22.6%	22.9	28.5%	26.2 %

Figure 3.3. Average buzz rate in the two sub areas SW Baltic and Baltic Proper. The box represents upper and lower quartiles. The horizontal line is the median and the black dots are outliers.



3.1.2 Temporal analyses (diel phase differences)

Examples of diurnal activity patterns from two stations with very different detection rates of harbour porpoises are shown in **Figure 3.4**.

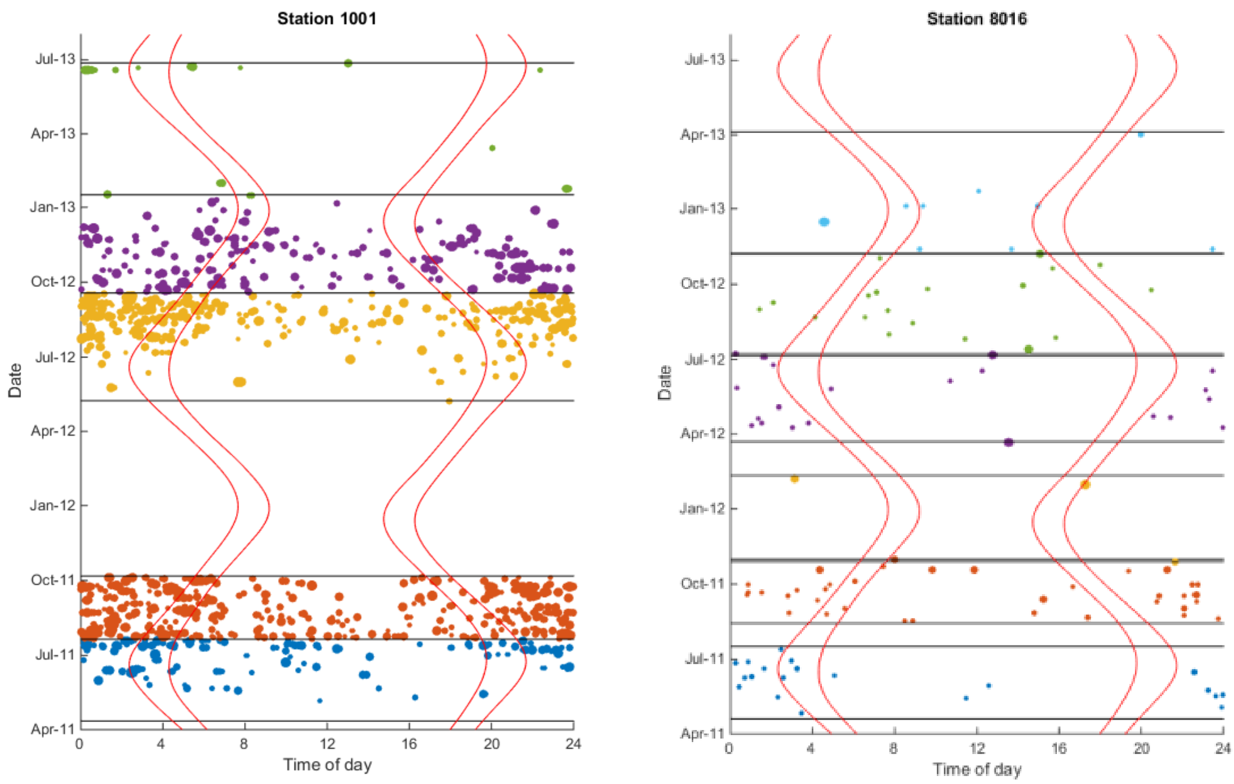
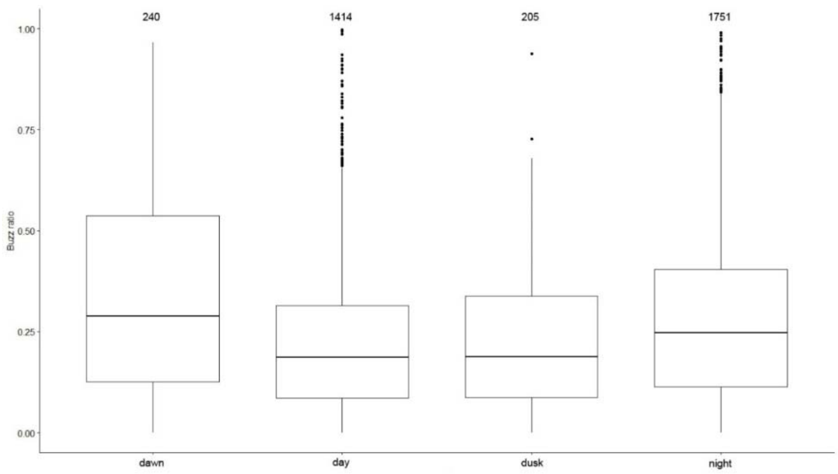


Figure 3.4. Examples of distribution of clicks in the different diel phases at two stations. The red lines signifies start and end of twilight, i.e. from left to right: night, dawn, day, dusk and night. The different colors of the dots signify different deployment periods.

Buzz ratio per diel phase displayed a clear diel pattern (Kruskal-Wallis chi-squared = 83.044, df = 3, n = 3610, p-value < $2.2e^{-16}$) (Table 3.2. and Figure 3.5.).

Figure 3.5. Box plot of buzz ratios for the four diel phases in the entire study area. Black line shows median buzz ratio per diel phase. The box includes the lower and upper quartiles. The black dots are outliers. A Wilcoxon ran sum test showed significant differences between some diel phases (**Table 3.2**).



A pairwise comparison using the *Wilcoxon rank sum test* showed significant differences between some of the diel phases with highest buzz ratios during dawn and night, n = 3486 (**Table 3.2**).

Table 3.3. Significant differences between diel phases for all data. Significant results from a Wilcoxon rank sum test.

Pairwise comparison	p-value
Dawn-day	<0.001
Dawn-dusk	<0.001
Dawn-night	0.004
Day-night	<0.001
Dusk-night	0.001

The diel phases within each of the sub areas were also compared. In the SW Baltic, there are differences in buzz ratio between diel phases (Kruskal-Wallis chi-squared = 66.416, df = 3, n = 3684, p-value = 2.497e-14) (**Figure 3.6**). Significant differences are displayed in **Table 3.4**.

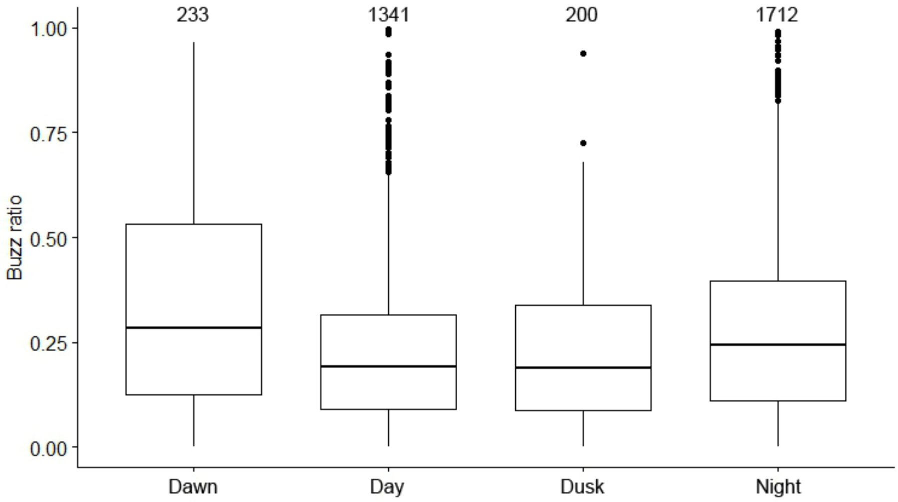


Figure 3.6. Box plot of buzz ratios for the four diel phases in the SW Baltic. Black line shows median buzz ratio per diel phase. The box includes lower and upper quartiles. The black dots are the outliers. Buzz ratio per diel phase were compared in a Wilcoxon rank sum test where the significant results are given in **Table 3.4**.

Table 3.4. Significant differences from the pairwise comparisons between diel phases in the South West with a Wilcoxon rank sum test.

Pairwise comparison	p-value
Dawn-day	<0.001
Dawn-dusk	<0.001
Dawn-night	0.005
Day-night	<0.001
Dusk-night	0.005

In the Baltic Proper, there are differences in buzz ratio between diel phases (Kruskal-Wallis chi-squared = 52.235, n=124, df = 3, p-value = 2.669e-11) (**Figure 3.7**). A Wilcoxon rank sum test showed were the differences were significant (**Table 3. 5**). The fewer significant differences are probably due to the fact that there are only 124 data points for the Baltic Proper, while there are 3486 data points in the SW. In the boxplot (**Figure 3.7**) the differences look even clearer than for the SW.

Table 3. 5. Significant results from the pairwise comparison between diel phases in the Baltic Proper.

Pairwise comparison	p-value
Dawn-day	<0.013
Day-night	<0.001
Dusk-night	0.005

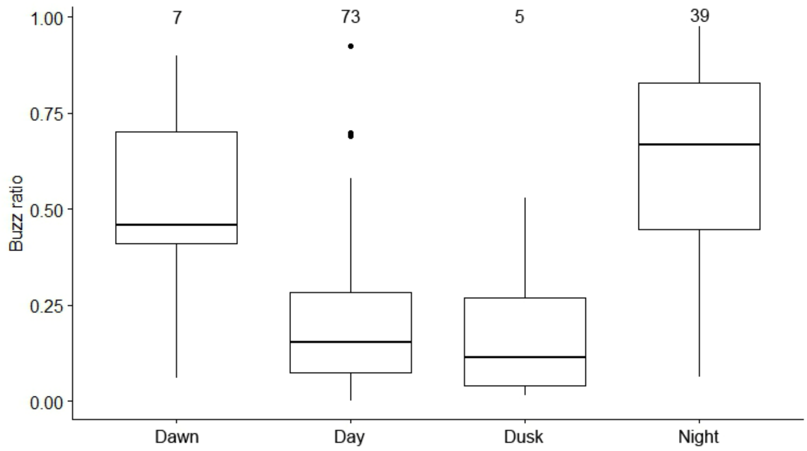


Figure 3.7. Box plot of buzz ratios for the four diel phases in the Baltic Proper. Black line shows median buzz ratio per diel phase and boxes are upper and lower quartiles. Buzz ratio per diel phase were compared in a Wilcoxon rank sum test where the significant results are given in **Table 3. 5**.

Overall, the highest buzz ratios were observed at dawn and night in the Baltic Proper with 51.9 and 61.6 % buzz clicks as opposed to 34.2 and 27.7 % in the SW Baltic, respectively (**Table 3.1**).

4. Discussion

By automating extraction of feeding buzzes from the large SAMBAH dataset, we have shown that the feeding ratio for harbour porpoises is higher in the Baltic Proper than in the SW Baltic, and that in the entire SAMBAH study area, the feeding buzz ratio is significantly higher during dawn and night than during the day and dusk. We could not identify forging areas within the high-density areas for harbour porpoises, which supports the theory that porpoises have to feed almost constantly and hence they occur where they can feed.

The random forest models showed that diel phase was clearly the most important variable in explaining the spatio-temporal distribution of feeding buzzes. None of the spatial variables such as depth or even geographical position had much effect on the models' ability to describe the distribution of higher feeding buzz ratios. Our interpretation is that there are only a weak spatial pattern in feeding buzz activity, and that harbour porpoises feed throughout their distribution range, or conversely, that they are distributed where they can feed. This is in line with previous studies suggesting that porpoises forage more or less continuously and thus will look for food wherever they may be (Wisniewska et al., 2016). It is very likely that their distribution range is strongly influenced by the presence of feeding areas; i.e. that porpoises tend to occur where the prey is and that the important foraging areas for porpoises coincide with the high-density areas as a whole. This result indicates that there are no specific areas in the Baltic where porpoises spend proportionally more of their time foraging than others, but that densities of porpoises likely reflect the underlying prey density.

Altogether, the results underline why harbour porpoises rightly are placed on the Habitat Directive's Annex IV, implying that the animals should be protected throughout their distribution range. This may seem to be in conflict with the requirements of Annex II to designate areas of special importance for the species. However, the indications that lead to the conclusion that porpoises are feeding almost continuously must then mean that the most important areas for foraging are also the areas where the highest densities are found. This is in contrast to for example seals, which spend considerable time travelling between foraging and resting areas, and larger cetaceans, which may go for months without foraging. Based on this, it appears that the best foundation for designating special areas of importance for harbour porpoises is simply where the density of animals is highest (in line with what has been done in for example Denmark (Sveegaard et al., 2011), Germany (Gilles et al., 2011) and Sweden (Carlström and Carlen, 2016)), and protection of and efficient conservation measures within such areas are at the same time most important and central for the positive development of a harbour porpoise population.

The buzz ratio was compared between the SW Baltic and the Baltic Proper and revealed a significant difference between the two clusters: a higher buzz ratio in the Baltic Proper, and lower in the SW Baltic. The underlying factors responsible for this difference can only be speculated upon. One such speculation could be a lower quality of prey, requiring an increased feeding rate in the Baltic Proper. This is in line with a recent study showing a positive correlation between blubber thickness of grey seals (*Halichoerus grypus*) and herring (*Clupea harengus*) quality across the Baltic Sea. The blubber thickness of all age groups of seals was thinnest in the Bothnian Bay where also herring weight was lowest. Contrary, a negative correlation was found between seal blubber thickness and herring catch size, a measurement of herring quantity (Kauhala et al., 2017). Another potential cause for the higher buzz ratio of harbour porpoises in the Baltic Proper is that the two populations have different preferred prey resulting in adapted feeding behaviours.

Our results show a clear temporal pattern with preferred diel phases for feeding. Feeding events across the year occurred more often at dawn and night, than during day and dusk. This pattern is a new finding for the Baltic Proper, and is similar to previous PAM studies elsewhere (Carlstrøm, 2005; Nuuttila et al., 2018; Schaffeld et al., 2016; Todd et al., 2009). Periods of darkness was also found in a tagging study to be when porpoises predominantly foraged with "prey encounter rates of 0–200 / hour during the day and 50–550 / hour after dusk" (Wisniewska et al., 2016). The pronounced diel pattern is likely to be a reflection of similar patterns in behaviour and / or diel vertical distribution of the prey of porpoises. However, such links have not been firmly established. The number of detected buzzes is much lower in CPOD data than in Dtag data. This is likely due to two factors. 1) The SAMBAH CPODs were placed close to the bottom and porpoises foraging in the middle or upper part of the water column was therefore not detected by the CPOD, especially not in deeper waters. 2) the conservative filtering of CPOD data may have reduced the number of included buzzes, compared to the D-tag data, which is blessed with a significantly better signal-to-noise ratio than C-POD recordings.

Feeding events are signified by a higher number of short ICIs, in relation to longer ICIs. In this study ICIs less than 15 ms were defined as arising from foraging buzzes, and ICIs longer were defined as from search phase echolocation. However, several confounding factors could possibly skew the number of short ICI events up or down (summarized in **Figure 3. 8**):

- If the area has a low density of prey, porpoises have to increase the search time, i.e. spend more time clicking in search phase, for each caught prey. This will reduce the buzz ratio for each caught prey, or, in a unit that really matters to the animals, per ingested kilojoule of energy. Because of this, one would predict a lower buzz ratio in areas with lower prey density.
- In areas with poor prey quality, porpoises will need to catch and eat more prey items to keep the caloric intake constant. This would increase the foraging rate, which could lead to an increase in buzz ratio. However, this is under the presumption that the animal will spend less time on other activities, and through that reduce the use of low-repetition rate clicks (search phase and navigation).
- If the prey capture success rate is low (for any reason), the porpoises will have to increase the number of foraging events to ingest the same caloric value, and the buzz ratio will increase.
- The prey species, its distribution and its behaviour may also affect the buzz ratio. Buzzes from prey captures higher up in the water column are likely to be less detectable for a bottom mounted PAM device than buzzes from bottom-foraging porpoises. Detection of the more powerful clicks of the search phase should be less affected, leading to a change in the buzz ratio. The high ratio of buzzes in the Baltic Proper could therefore be due to prey being dispersed more favourable for PAM detection than in the SW Baltic, meaning that the prey predominantly should be dispersed near the bottom in the Baltic Proper.

- Lastly, porpoise communication calls also have high-repetition rate click trains, resembling those of feeding buzzes (Sørensen et al., 2018). Sørensen et al. (2018) studied acoustic behaviours of wild harbour porpoises in Inner Danish Waters using acoustic and behavioural tags mounted on the animals. They found that porpoises emit communication calls and that the source level of the clicks in these calls is up to 10 dB higher than during buzzing. The click repetition rate of calls (85-330 clicks / s, i.e. 3.0-11.8 ms ICIs) were found to be either higher (<1000 clicks / s, i.e. <1 ms ICI) or overlapping with the click repetition rate of observed feeding buzzes (260-360 clicks / s, i.e. 2.8-3.8 ms ICI). The lowest ICIs were found in mother-calf pairs that had been separated (1000 clicks / s, or 1 ms ICIs). Regular clicking had ICIs over 100 ms. Between 7.7 and 31.5 % of the recorded minutes on six tag deployments contained calls. About 10 % of the time calls were also recorded from nearby animals. The study therefore shows that harbour porpoises are much more vocally in contact than can be visually observed from their surface behaviour. In this study we defined buzzes as being of lower ICI than 15 ms. It is therefore very likely that some of the extracted buzzes in fact were communication calls, and in an area or period with highly communicating porpoises, the buzz ratio is expected to increase. Yet, based on the low density of porpoises in the Baltic Proper, a low number of communication calls is expected to have been included there. **Figure 3. 8** summarizes the possible drivers for high and low buzz ratios.

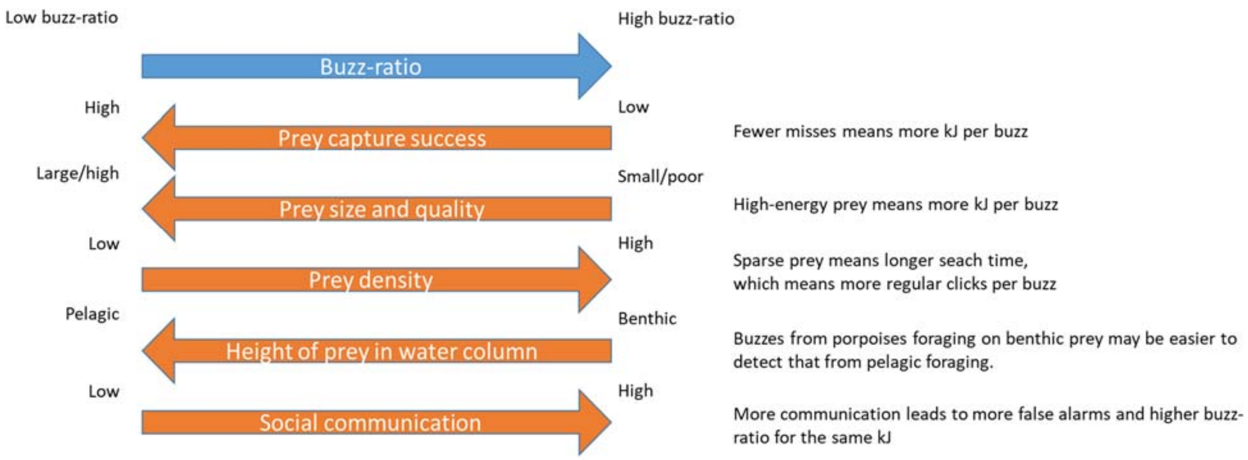


Figure 3. 8. Relationships between potentially confounding factors and buzz ratio.

We do not know the relative importance of these confounding factors in the present study, and thus cannot assess to what extent they may have skewed the results. Regardless of the underlying cause, a much higher ratio of buzz ICIs were found in the Baltic Proper at Hoburg's Bank and the Northern and Southern Mid-sea Banks, confirming that this area is important both in terms of density and foraging.

4.1 Conclusion

This study shows a high buzz ratio of harbour porpoises throughout their high density areas, indicating that they forage wherever they are, or conversely, they are where they can forage. For the critically endangered Baltic Proper population, this implies that the area around Hoburg's Bank and the Northern and Southern Mid-sea Banks not only is the area with highest densities of harbour porpoises, but also their most important foraging area. The buzz ratio in the SW Baltic is somewhat lower than at the offshore banks, but consistent with no spatial pattern of buzzes within the area. The results underline the importance of the Habitats Directive, Annex IV; that a system of strict protection should be implemented throughout the harbour porpoise's distribution range, and supports Annex II stating that areas of significant importance for the species should be protected. Our data supports that such areas are best appointed based on the density of harbour porpoises.

In order to increase the chances for a positive development of the critically endangered Baltic Proper harbour porpoise population, management plans with actual conservation measures should be implemented for the designated Natura 2000 sites.

References

ASCOBANS. 2016. ASCOBANS Recovery Plan for Baltic Harbour Porpoises.

Benjamini, Y. and Y. Hochberg. 1995. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *J R Stat Soc Series B Stat Methodol.* 57(1), 289-300.

Benjamins, S., N. van Geel, G. Hastie, J. Elliott, and B. Wilson. 2017. Harbour porpoise distribution can vary at small spatiotemporal scales in energetic habitats. *Deep Sea Research Part II: Topical Studies in Oceanography*. 141:191-202.

Bouchet, P.J., Meeuwig, J.J., Salgado Kent, C.P., Letessier, T.B., Jenner, C.K., 2015. Topographic determinants of mobile vertebrate predator hotspots: current knowledge and future directions: landscape models of mobile predator hotspots. *Biol. Rev*. 90, 699–728.

Breiman, L. 2001. Random forests. *Machine learning*. 45:1, 5-32.

Carlén, I., L. Thomas, J. Carlström, M. Amundin, J. Teilmann, N. Tregenza, J. Tougaard, J.C. Koblitz, S. Sveegaard, D. Wennerberg, O. Loisa, M. Dähne, K. Brundiers, M. Kosecka, L.A. Kyhn, C.T. Ljungqvist, I. Pawliczka, R. Koza, B. Arciszewski, A. Galatius, M. Jabbusch, J. Laaksonlaita, J. Niemi, S. Lyytinen, A. Gallus, H. Benke, P. Blankett, K.E. Skóra, and A. Acevedo-Gutiérrez. 2018. Basin-scale distribution of harbour porpoises in the Baltic Sea provides basis for effective conservation actions. *Biological Conservation*. 226:42-53.

Carlström, J. 2005. Diel variation in echolocation behaviour of wild harbour porpoises. *Mar Mamm Sci*. 21:1-12.

Carlström, J., and I. Carlen. 2016. Skyddsvärda områden för tumlare i svenska vatten. *In* AquaBiota Report. Vol. 04. AquaBiota, Stockholm.

Carroll, C., Noss, R.F., Paquet, P.C., 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. *Ecol. Appl*. 11, 961–980.

Carstensen, J., J.H. Andersen, B.G. Gustafsson, and D.J. Conley. 2014. Deoxygenation of the Baltic Sea during the last century. *Proceedings of the National Academy of Sciences*. 111:5628-5633.

Cutler, D.R., T.C. Edwards Jr, K.H. Beard, A. Cutler, K.T. Hess, J. Gibson and J.J. Lawler. 2007. Random forests for classification in ecology. *Ecology*. 88(11), 2783-2792

Dickson, B.G., Beier, P., 2007. Quantifying the influence of topographic position on cougar (*Puma concolor*) movement in southern California, *USA. J. Zool*. 271, 270–277. https://doi.org/10.1111/j.1469-7998.2006.00215.x.

Gilles, A., S. Adler, K. Kaschner, M. Scheidat, and U. Siebert. 2011. Modelling harbour porpoise seasonal density as a function of the German Bight environment: implications for management. *Endangered Species Research*. 14:157-169.

Hammond, P.S., Bearzi, G., Bjørge, A., Forney, K.A., Karczmarski, L., Kasuya, T., Perrin, W., Scott, M.D., Wang, J.Y. , Wells, R.S. & Wilson, B. 2008. Phocoena phocoena (Baltic Sea subpopulation) (errata version published in 2016). The IUCN Red List of Threatened Species 2008: e.T17031A98831650. Http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T17031A6739565.en.

Hansson, M., and L. Andersson. 2016. Oxygen Survey in the Baltic Sea 2015 : Extent of Anoxia and Hypoxia, 1960-2015. The major inflow in December 2014. *In* RO, Rapport Oceanografi. SMHI. 8.

Hollander, M., D.A. Wolfe and E. Chicken. 2013. Nonparametric statistical methods. John Wiley & Sons.

Kauhala, K., Bäcklin, BM., Raitaniemi, J., Harding, KC. 2017. *Mamm Res* 62: 351. https://doi.org/10.1007/s13364-017-0329-x

Kyhn, L.A., J. Tougaard, K. Beedholm, F.H. Jensen, E. Ashe, R. Williams, and P.T. Madsen. 2013. Clicking in a Killer Whale Habitat: Narrow-Band, High-Frequency Biosonar Clicks of Harbour Porpoise (*Phocoena phocoena*) and Dall's Porpoise (*Phocoenoides dalli*). *PLoS ONE 8*. 58.

Miller, L.A., J. Pristed, B. Møhl, and A. Surlykke. 1995. The Click-Sounds of Narwhals (*Monodon monoceros*) in Inglefield Bay, Northwest Greenland. *Mar. Mamm. Sci.* 11:491-502.

Nuuttila, H.K., C.M. Bertelli, A. Mendzil, and N. Dearle. 2018. Seasonal and diel patterns in cetacean use and foraging at a potential marine renewable energy site. *Marine Pollution Bulletin*. 129:633-644.

Pirotta, E., K.L. Brookes, I.M. Graham, and P.M. Thompson. 2014. Variation in harbour porpoise activity in response to seismic survey noise. *Biological Letters* 10:20131090.

Schaffeld, T., S. Bräger, A. Gallus, M. Dähne, K. Krügel, A. Herrmann, M. Jabbusch, T. Ruf, U.K. Verfuß, H. Benke, and J.C. Koblitz. 2016. Diel and seasonal patterns in acoustic presence and foraging behaviour of free-ranging harbour porpoises. *Marine Ecology Progress Series*. 547:257-272.

Sørensen, P.M., D.M. Wisniewska, F.H. Jensen, M. Johnson, J. Teilmann, and P.T. Madsen. 2018. Click communication in wild harbour porpoises (Phocoena phocoena). *Scientific Reports*. 8:9702.

Sveegaard, S., J. Teilmann, J. Tougaard, R. Dietz, K.N. Mouritsen, G. Desportes, and U. Siebert. 2011. High-density areas for harbor porpoises (Phocoena phocoena) identified by satellite tracking. *Marine Mammal Science*. 27:230-246.

Todd, V.L.G., W.D. Pearse, N.C. Tregenza, P.A. Lepper, and I.B. Todd. 2009. Diel echolocation activity of harbour porpoises (Phocoena phocoena) around North Sea offshore gas installations. *ICES Journal of Marine Science*. 66:734-745.

Tregenza, N. 2013. Tregenza, N. 2013. Validating cetacean detections. http://www.chelonia.co.uk/cpod_downloads.htm.

Verfuß, U.K., L.A. Miller, P.K.D. Pilz, and H.U. Schnitzler. 2009. Echolocation by two foraging harbour porpoises (*Phocoena phocoena*). *Journal of Experimental Biology*. 212:823-834.

Villadsgaard, A., M. Wahlberg, and J. Tougaard. 2007. Echolocation signals of wild harbour porpoises, *Phocoena phocoena*. *J Exp Biol*. 210:56-64.

Williams, T.M., and J.L. Maresh. 2016. Exercise Energetics. *In* Marine Mammal Physiology. Vol. 1. M. Castellini and J.A. Mellish, editors. CRC Press, Boca Raton. 376.

Wisniewska, D.M., M. Johnson, K. Beedholm, M. Wahlberg, and P.T. Madsen. 2012. Acoustic gaze adjustments during active target selection in echolocating porpoises. *The Journal of Experimental Biology*. 215:4358-4373.

Wisniewska, D.M., M. Johnson, J. Teilmann, L. Rojano-Donate, J. Shearer, S. Sveegaard, L.A. Miller, U. Siebert, and P.T. Madsen. 2016. Ultra-High Foraging Rates of Harbor Porpoises Make Them Vulnerable to Anthropogenic Disturbance. *Curr Biol*. 26:1441-1446.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14.

[Blank page]

BALHAB

Project report to ASCOBANS for the project “Baltic Sea Harbour porpoise foraging habitats (BALHAB)“

The harbour porpoise is protected by the Habitats Directive Annexes II and IV. This means that a system of strict protection shall be established throughout its natural range (Annex IV), and that sites of significant importance to the species should be designated and protected (special areas of conservation) (Annex II). Preferred foraging habitats could be considered candidates for special areas of conservation. Here we investigated whether foraging areas can be identified in the acoustic data from the SAMBAH project. Feeding buzzes were extracted from the SAMBAH dataset. Feeding buzz ratio was higher in the Baltic Proper than in the SW Baltic. In the entire SAMBAH study area, the feeding buzz ratio was significantly higher during dawn and night. Specific foraging areas within the high-density areas was not found, supporting the theory that porpoises have to feed almost constantly and that porpoises occur where they can feed.

ISBN: 978-87-7156-353-5
ISSN: 2245-0203